# HANDBOOK OF CANADIAN MAMMALS

## 2 Bats

C.G. van Zyll de Jong



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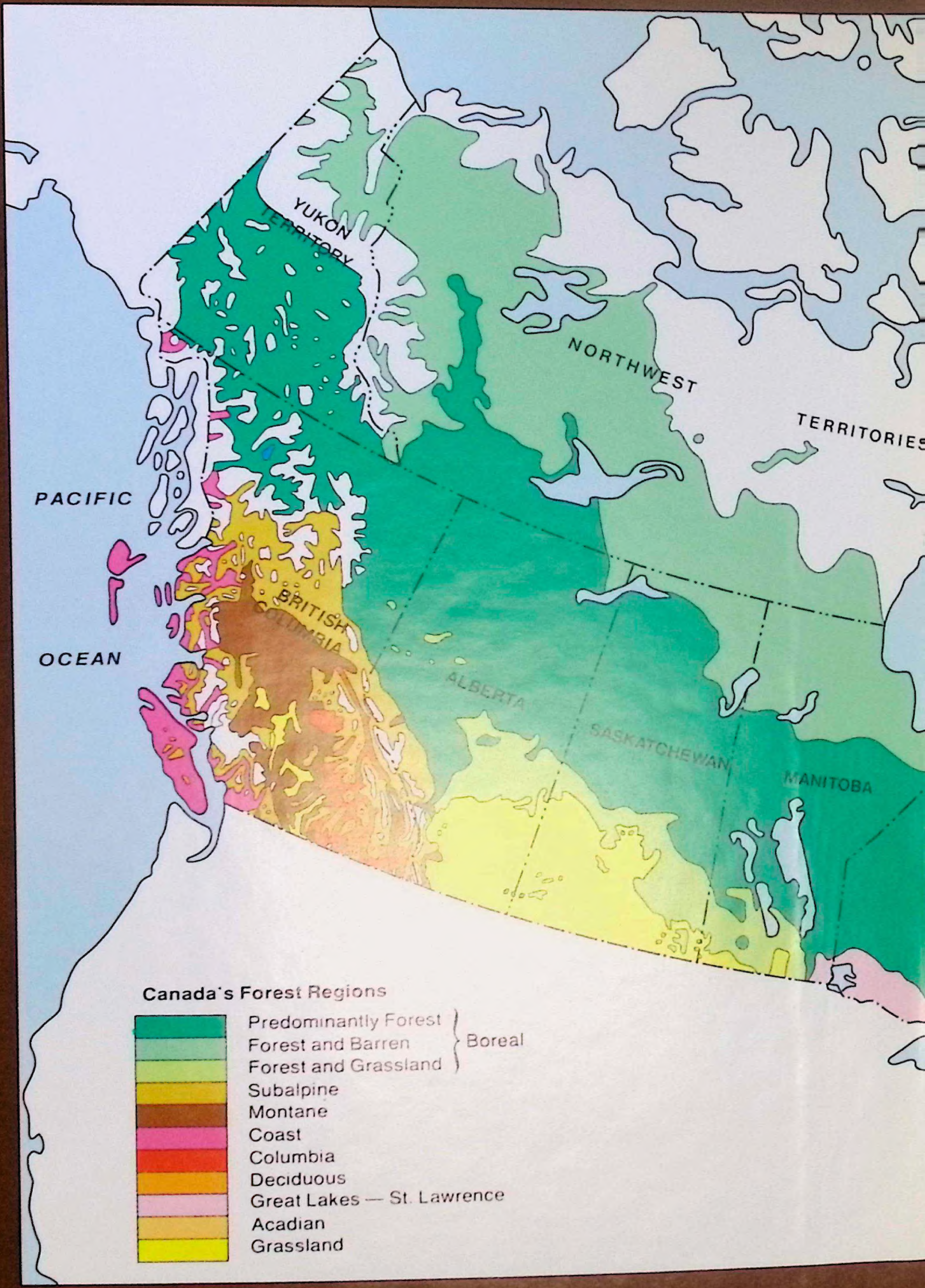
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Canada's Forest Regions
Predominantly Forest
Forest and Barren
Forest and Grassland
Boreal
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Montane
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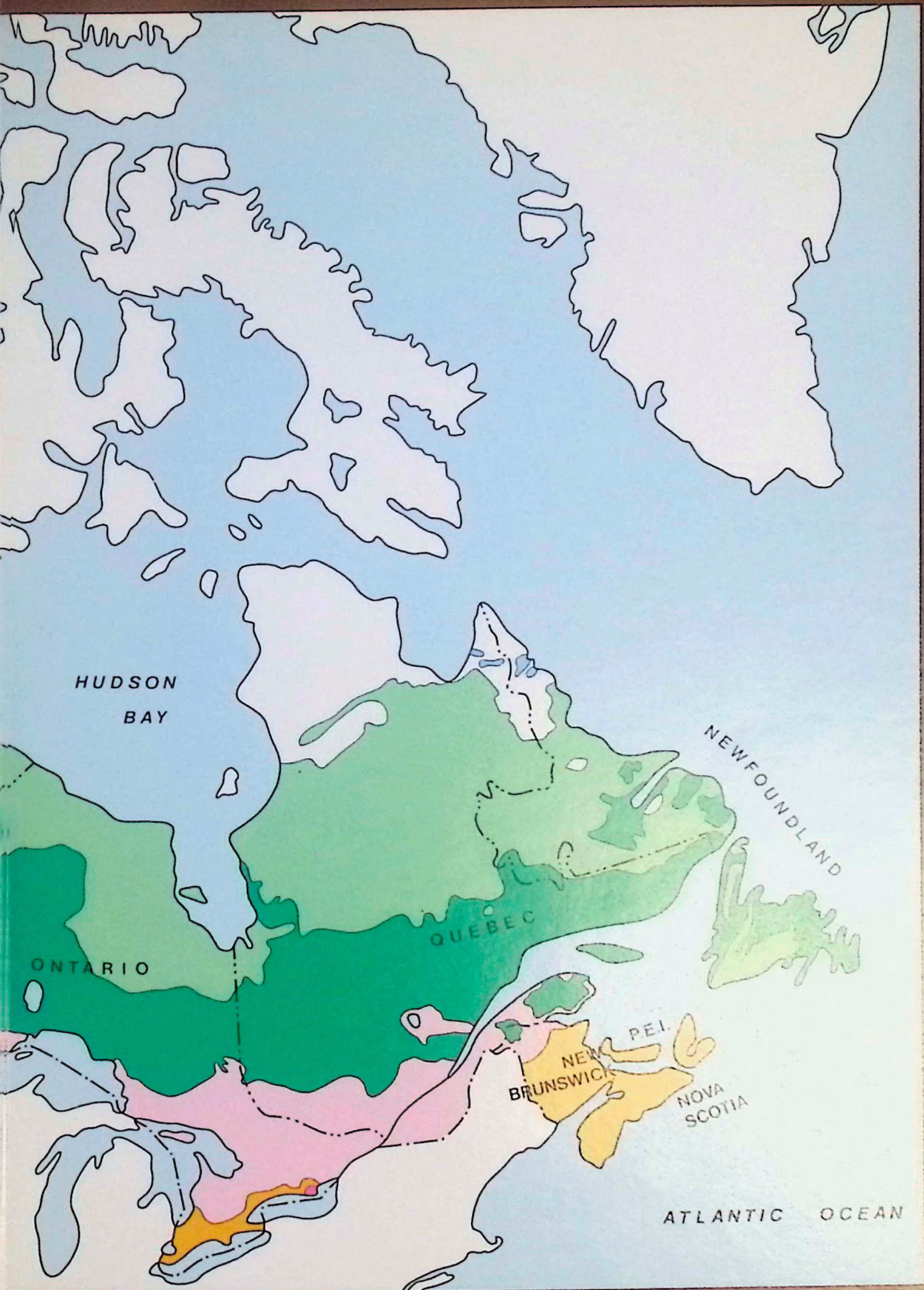
Columbia
Deciduous
Great Lakes — St. Lawrence
Acadian
Grassland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## 2 Bats

**C.G. van Zyll de Jong**

Coloured Illustrations
Paul Geraghty

Drawings
C.H. Douglas
Paul Geraghty
Donna Naughton

Maps
Donna Naughton

**National Museum of Natural Sciences**
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National Museum of Natural Sciences
National Museums of Canada
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This book is dedicated to Randolph L. Peterson in recognition of his important contributions to mammalogy in Canada and to the systematics of bats.

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# ACKNOWLEDGEMENTS

The colour plates and some of the black-and-white drawings were done by Mr. Paul Geraghty, whose work speaks for itself and contributes much to the attractiveness of this volume. The splendid illustrations of skulls are from the hand of Mr. Charles Douglas, whose patience in reproducing the subtle details was much appreciated. I am indebted to Ms. Donna Naughton for her painstaking preparation of the distribution maps, assistance in compiling the bibliography and measurements and in drafting a number of line drawings and graphs. Mr. David Campbell assisted with the compilation of distributional data and literature and in numerous other ways. I am grateful to Dr. Henri Ouellet for his help in coining and verifying French names. I am most grateful to my colleagues, Dr. M.B. Fenton and Dr. T.H. Kunz, who critically read and commented on the manuscript. Finally I acknowledge the kind cooperation of the following persons who gave me access to collections and specimens or who provided information on distribution: M.B. Fenton, S. Gorham, C.J. Guiguet, M.L. Leonard, D.W. Nagorsen, R.L. Peterson, W.E. Roberts, D.B. Schowalter, F. Scott, H.C. Smith, J.E. Storer, M.E. Taylor and R.E. Wrigley.

# INTRODUCTION TO VOLUME 2

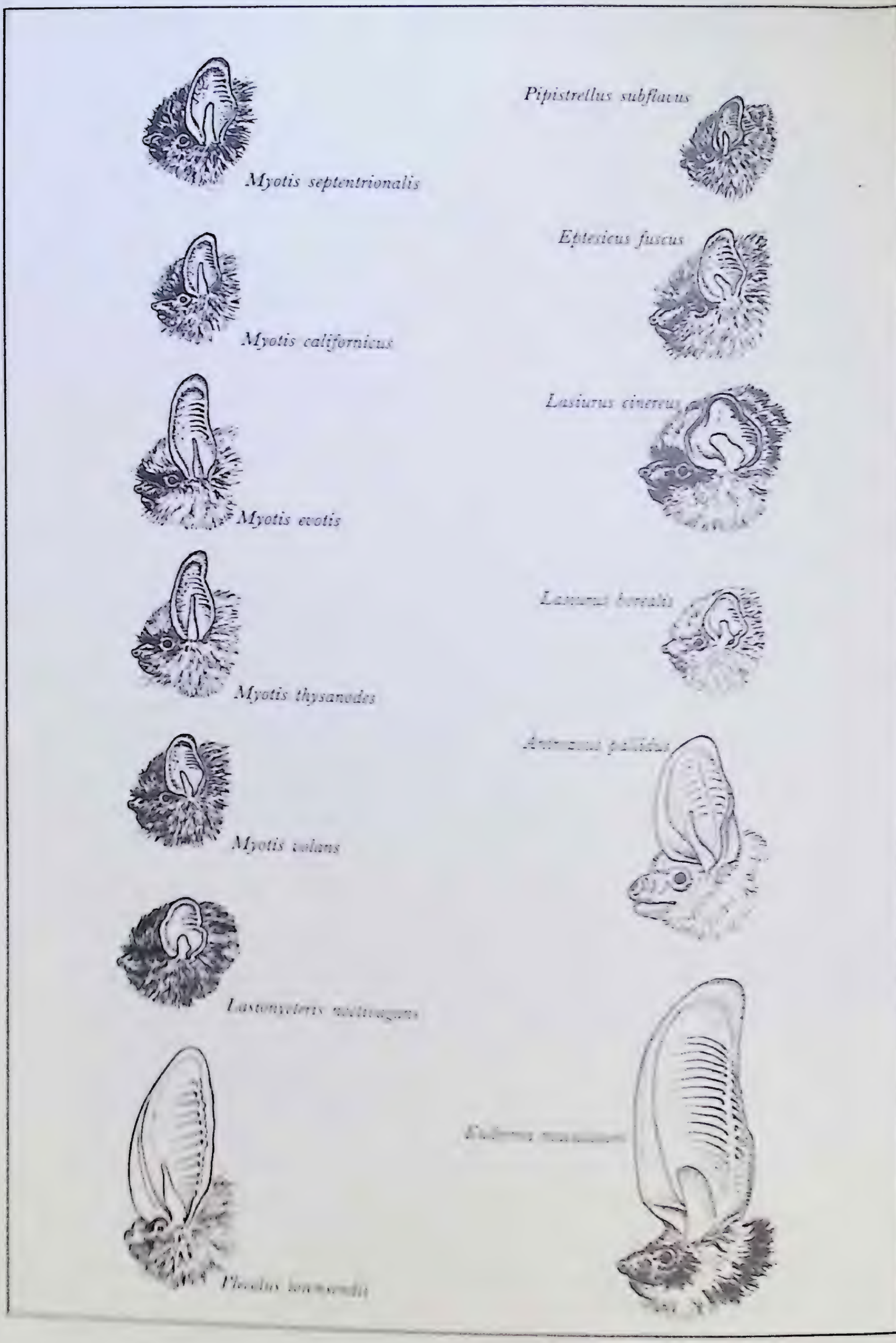
This volume differs from the preceding volume chiefly in the more extensive treatment of some aspects of the general biology of the order to which this volume is devoted. The reasons for this expanded treatment are the unique adaptations of the Chiroptera and the wealth of available information on their biology on the one hand and the dearth of information on many of our native species on the other.

The nocturnal volant way of life of bats has had a profound influence on several aspects of their biology, which in many ways diverges from the usual mammalian pattern. The success of the group, which finds expression in the great diversity of species, varied trophic adaptations, great numerical abundance and worldwide distribution, is in no small measure linked to the basic adaptation of flight. Since the early work on echolocation by Griffin and Galambos (1940), which sparked great interest in the study of bats, research on many aspects of the biology of these animals has increased by leaps and bounds so that at present there exists an extensive and ever-growing literature on the group. Despite this trend most species, including most of our native bats, remain poorly known. In view of this, I have provided a brief general introduction to some of the important aspects of the biology of bats. However, this book focuses on systematics, distribution and biology of bats in Canada, and is not a comprehensive treatise on bat biology.

The systematic, ecological and behavioural aspects of the biology of bats are emphasized, wherever possible using native species as examples, but at the same time giving a hint of the worldwide perspective. For those readers who want to delve a bit deeper, the references listed at the end of the general section on the Chiroptera will show the way to further literature.

Because of the difficulties of studying bats in the field, research on this group lagged behind that of other mammals until special techniques, including methods of live capture, and special electronic equipment were developed. Until recently, therefore, few people in Canada studied bats. Aside from basic information on taxonomy, distribution and isolated observations on biology and behaviour, no long-term, intensive research on Canadian bats was done until the introduction of banding. Harold Hitchcock started banding bats in Ontario and Quebec in the late 1930s and continued until 1961. The introduction and development of live-capture devices (mist nets, bat traps) and electronic equipment (''bat detectors'') broadened the possibilities for studying bats in their natural surroundings and shifted the emphasis to the study of ecology and behaviour. In Canada the most outstanding contributions to the study of these aspects of our native bats have been made by M.B. Fenton and his students in the 1970s and up to the present, mostly in eastern Canada but recently also in the west. In western Canada, D.B. Schowalter and his co-workers have made important contributions to our knowledge of the local bat fauna.

A detailed discussion of the various techniques and different types of equipment used in studying bats is not within the scope of this book. Those interested in information on this subject are advised to read the last chapter of Barbour and Davis (1969, *Bats of America*) as a general introduction. For information on the study of echolocation and ultrasonic apparatus, Busnell and Fish (1980, *Animal Sonar Systems*) and Simmons *et al.* (1979, *Apparatus for*


Myotis septentrionalis
Pipistrellus subflavus
Myotis californicus
Eptesicus fuscus
Lasiurus cinereus
Myotis evotis
Lasiurus borealis
Myotis thysanodes
Antrozous pallidus
Myotis volans

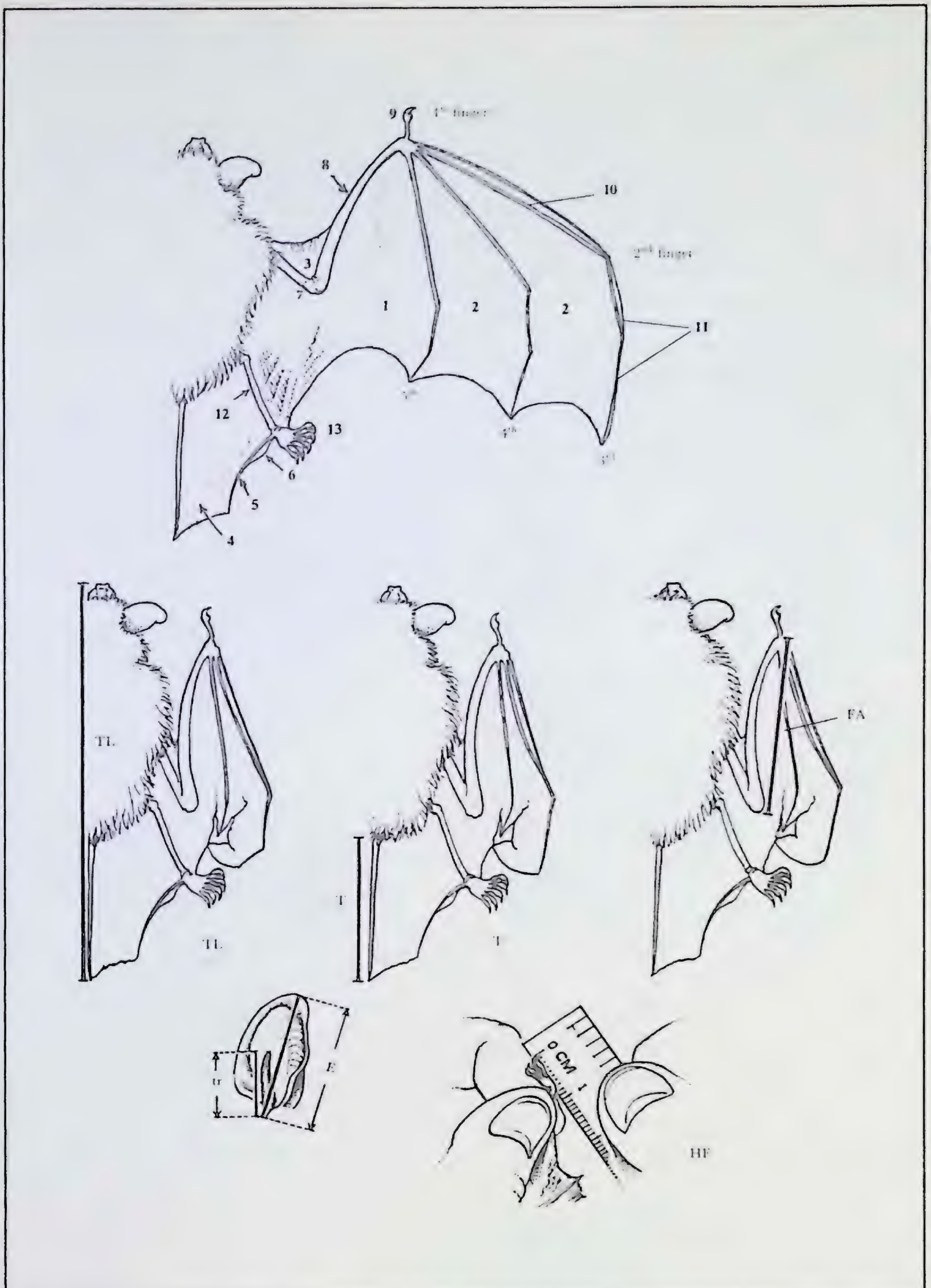
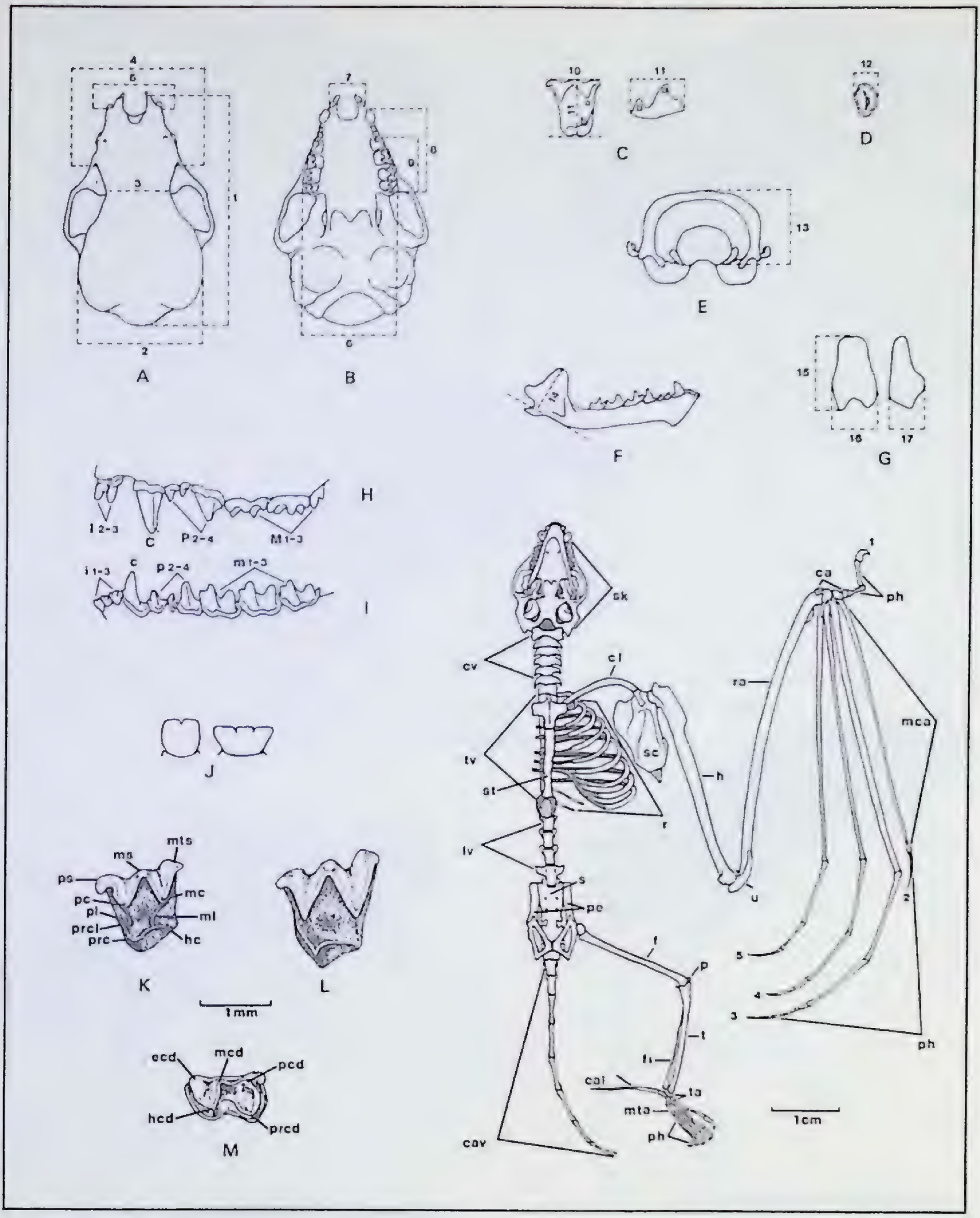



Figure 1. External topography of a vespertilionid bat, standard measurements and ears of different Canadian bats. 1) plagiopatagium; 2) chiropatagium; 3) propatagium; 4) uropatagium; 5) calcar; 6) keel of calcar; 7) upper arm; 8) forearm; 9) thumb; 10) metacarpals; 11) phalanges; 12) tibia; 13) foot. TL = total length; T = length of tail; FA = length of the forearm; E = length of the ear; tr = tragus; HF = length of the foot.

Figure 2. Skull measurements, dentition and skeleton of a vespertilionid bat. Skull measurements: A and B, Dorsal and ventral view of the cranium: 1) length of the skull (SL); 2) mastoid width (MW); 3) least interorbital width (IOW); 4) orbital width at the lacrimal foramina (OWL); 5) rostral width immediately posterior to the canines (RW); 6) maxillary width at M3 (M3M3W); 7) width of the upper incisors (I3I3W); 8) length of the maxillary tooth row (MTL); 9) length of P4M3 (P4M3L); C, Occlusal and lateral view of M2: 10) length of M2 (M2L); 11) width of M2 (M2W); D, Occlusal view of canine: 12) basal width of the upper canine at the cingulum (CW); E, Posterior view of cranium: 13) cranial depth (CD); F, Mandible: 14) height of the coronoid process (HCP). Dentition and tooth topography: G, Baculum measurements: 15) length, 16) width, 17) height; H and I, Upper and lower left tooth row of *Myotis*, capitals are used for upper, lower case of lower teeth, I, i = incisors; C, c = canine; P, p = premolars; M, m = molars; J, 1) bifid lower incisor of a molossid; 2) trifid lower incisor of a vespertilionid. Topography of upper and lower molar: K, Occlusal view of left M2 of *M. lucifugus*: hc = hypocone; mc = metacone; ml = metaloph; ms = mesostyle, mts = metastyle; pc = paracone; pl = paraloph; prc = protocone; prcl = protoconule; ps = parastyle; L, Occlusal view of left M2 showing the simplified pattern found in the subgenus *Myotis* (most extreme in *M. thysanodes* among native bats) ml, pl and prcl are absent and hc is reduced (abbreviations as in K); M, Occlusal view of left m2 of *M. lucifugus*: ecd = entoconid; hcd = hypoconid; mcd = metaconid; pcd = paraconid; prcd = protoconid. Skeleton (*Eptesicus*): ca = carpals; cal = calcar; cav = caudal vertebrae; cl = clavicle; cv = cervical vertebrae; f = femur; fi = fibula; h = humerus; lv = lumbar vertebrae; mca = metacarpals; mta = metatarsals; pe = pelvis; ph = phalanges; r = ribs; ra = radius; s = sacrum; sc = scapula; sk = skull; st = sternum; t = tibia; ta = tarsals; tv = thoracic vertebrae; u = ulna; 1–5 = digits.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*Research on Animal Ultrasonic Signals*) are particularly good sources. Details on methodology of Chiropteran research can be found in the scientific journals cited in these references and in this volume. Information on current research on bats is published in newsletters such as *Bat Research News* (North America), *Myotis* and *Nyctalus* (Europe).

The English common names in this book are those most often used in current North American literature, but for *Myotis septentrionalis* and *M. keenii*, which are here treated as separate species, new names were coined. As to the French names used in this volume, I have deviated from Bernard *et al.* (1967) and follow the practice of French-speaking European countries in using *Vespertilion* and *Sérotine* for all species of *Myotis* and *Eptesicus* respectively. One of the external measurements taken on bats, the length of the forearm (FA), differs from the usual standard measurements taken on small mammals. Forearm length (FA) is the best indicator of size in bats as it can be measured with a greater degree of precision than total length (TL). All measurements and weights in the text are in millimetres and grams respectively, unless stated otherwise. The measurements and weights given in each species account are based on samples of adult animals of both sexes from localities within the species' Canadian range. Where no or insufficient numbers of specimens from Canadian localities were available, specimens from localities in the United States were used or measurements were taken from the literature as noted. For Canadian specimens, samples from different parts of the range were pooled to encompass geographic variation. Where significant differences in size exist between different subspecies, these are noted in the discussion of subspecies where appropriate measurements are given. All measurements and abbreviations are defined and shown on the diagrams in Figures 1 and 2.


Colour Plate I

*Lasionycteris noctivagans*

*Eptesicus fuscus*

*Myotis septentrionalis*

*Myotis evotis*

*Myotis thysanodes*

*Myotis keenii*

Colour Plate II

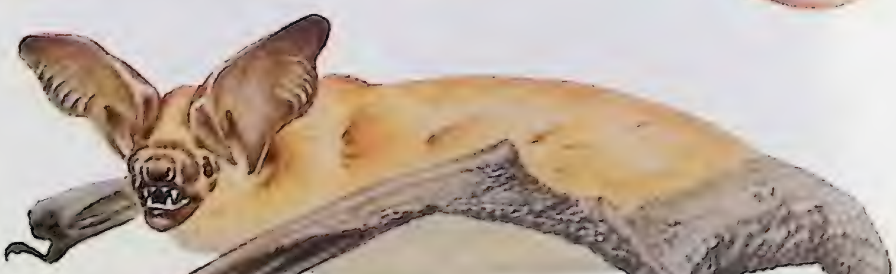
*Lasiurus cinereus*

*Lasiurus borealis*

Colour Plate III

*Plecotus townsendii*

*Euderma maculatum*



*Antrozous pallidus*

Colour Plate IV

# ORDER CHIROPTERA BLUMENBACH, 1779

(f. Gk *kheir* hand; *pteron* wing)

Bats | Chauves-souris

**General Characteristics**

The Chiroptera are characterized by forelimbs that are modified for true flight. The humerus and forearm and some bones of the hand are elongated to support a flight membrane of thin pliable skin. Usually only the first, but in some forms also the second digit, has claws. There are six carpals and five metacarpals. The first digit (the thumb) has two short phalanges. The next four fingers are long and thin. The second digit has one, two or three phalanges or consists only of a metacarpal; the third, fourth and fifth digits usually possess three phalanges. The distal phalanx of the third digit may be cartilagenous or ossified; in the third, fourth and fifth digit, the third phalanx is often absent. The humerus has no foramen entepicondyloideum. The radius is long and slender. The ulna is reduced, so that only proximal and distal ends remain.

The knee is directed outward due to a 90° rotation of the hind leg, and the foot has rotated 180° from the usual mammalian position so that it points backwards and facilitates a head-down suspension of the animal. The hind foot has five toes of approximately equal length, all bearing well-developed curved claws. The fibula is often rudimentary. The bones of the shoulder girdle and chest are well developed in contrast with the small pelvic girdle. The rib cage is dorsoventrally flattened and the sternum may have a small keel for the attachment of flight muscles. The clavicle also is well developed. The thoracic vertebrae fit tightly together to form a rigid structure in most bats. In some families the first thoracic and last cervical vertebra are fused.

The dentition is diphyodont and heterodont. There are never more than two upper incisors on each side. The cheek teeth vary greatly in cusp pattern according to the diet, but are derived from tritubercular, secodont teeth. The stomach is usually simple or double in some forms; the caecum is small or lacking. The penis is pendulous and usually has a baculum; testes are inguinal or abdominal, descending in a temporary peritoneal evagination (cremaster sack) or a scrotum. The uterus is duplex, bicornate or simple, the placenta discoidal and deciduate. There is usually one pair of pectoral, mostly axillary, mammae.

**Distribution**

The order is nearly cosmopolitan, being absent from the Arctic and Antarctic only. Frugivorous bats are restricted to the tropics and subtropics of both hemispheres, whereas insectivorous bats are found to the tree line. Bats are most abundant and diverse in the tropics, the Indo-Australian archipelago and the Neotropical Region having particularly rich chiropteran faunas, which account for approximately 30 and 24 per cent respectively of the species of bats found in the world. The abundance and diversity of bats decrease gradually toward the north and south from the tropics.

Table 1. The distribution of bats in major Canadian life-zone areas

| | *M. lucifugus* | *M. yumanensis* | *M. volans* | *M. keenii* | *M. septentrionalis* | *M. evotis* | *M. thysanodes* | *M. californicus* | *M. ciliolabrum* | *M. leibii* | *P. subflavus* | *L. borealis* | *L. cinereus* | *L. noctivagans* | *P. townsendii* | *E. maculatum* | *E. fuscus* | *N. humeralis* | *A. pallidus* | *T. macrotis* | Total number of species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Deciduous Forest Region | X | | | | X | | | | | X | X | X | X | X | | | X | A | | | 9 |
| Great Lakes–St. Lawrence Forest Region | X | | | | X | | | | | X | X | X | X | X | | | X | | | | 8 |
| Acadian Forest Region | X | | | | X | | | | | | X | X | X | X | | | X | | | | 7 |
| Coast Forest Forest Region | X | X | X | X | | X | | X | | | | | X | X | X | | X | | | A | 11 |
| Montane Forest Region | X | X | X | | | X | | | | | | A | X | X | X | | X | | | | 9 |
| Subalpine Forest Region | X | | X | | | X | | | | | | | X | X | | | X | | | | 6 |
| Columbia Forest Region | X | X | X | | X | X | | X | | | | | X | X | X | | X | | | | 10 |
| Boreal Forest | X | | | | X | | | | | | | X | X | X | | | X | | | | 6 |
| Forest-Grassland Transition | X | | | | X | | | | | | | X | X | X | | | X | | | | 6 |
| Forest-Tundra Transition | X | | | | | | | | | | | A | A | | | | | | | | 3 |
| Prairies | X | | | | | X | | | X | | | | X | X | | | X | | | | 6 |
| Southern British Columbia Arid Area | X | X | X | | | X | X | X | X | | | | X | X | X | X | X | | X | | 13 |
| Tundra | | | | | | | | | | | | A | A | | | | | | | | 2 |

X Resident for at least part of the year
A Accidental

## Distribution and Abundance of Canadian Bats

In Canada, bats are found in nearly all the major vegetation zones, with the exception of the tundra, where their occasional occurrence is probably accidental (Table 1). Of the four major components of the environment that determine the distribution and abundance of bats, climate, food, other animals (predators, competitors, etc.) and roosts, it is probably the first and the last that are most important. The greatest species diversity and population densities in Canada are found in the south and diminish toward the north. The northern limit of the distribution of bats coincides approximately with a zone with a mean annual growing season of 120 days, i.e. a period between spring and autumn in which the daily mean temperature is above 6°C. This period represents the minimum time required for a species such as *Myotis lucifugus* to produce and raise young and to build up energy reserves prior to hibernation. In the southern part of Canada, the species diversity, as well as the distribution and abundance of individual species, may be largely determined by the availability of suitable roosts (both summer and winter). High species diversity and population densities may be expected in areas where all types of roosts are found in abundance.

## Classification

The order Chiroptera is subdivided into two distinct suborders, the Megachiroptera and the Microchiroptera. The Megachiroptera differ from the Microchiroptera in many details, including the following characters: 1) the second finger remains relatively independent from the third and usually has a claw; 2) the humerus is relatively unspecialized in having relatively small greater and lesser tuberosities; 3) the external ear is simple and there is no tragus; 4) they rely predominantly on vision and olfaction to find their way and locate food. Some species of *Rousettus* are the only Megachiroptera capable of echolocation.

The Chiroptera are the largest mammalian order after the rodents, with 17 families, 175 genera and approximately 919 species [13]. The Megachiroptera comprise only one family with 161 species distributed in the tropical and subtropical regions of the Old World. The Microchiroptera contain 16 families with 758 species and are cosmopolitan (Table 2). Only two families and 20 species have been recorded from Canada.

## Evolution

Not much is known about the evolution of bats. The earliest known fossil bat, *Icaronycteris index*, dates from the Eocene of North America approximately 50 million years ago. This bat, aside from some primitive characters, differed little from living microchiropteran insectivorous bats. Earlier fossil skulls and teeth, from the Palaeocene about 60 million years ago, could have belonged to bats, or to early insectivores from which bats are generally assumed to have evolved. There is no unanimity at present on the question of whether the two suborders are monophyletic. Some scientists think that the Microchiroptera and Megachiroptera evolved independently from different insectivore ancestors, although a majority consider it more likely that the two originated from the same ancestral group but diverged at a very early time. The phylogenetic relationships among the chiropteran superfamilies remain unclear, although several phylogenetic analyses using various character complexes have been undertaken [15, 16]. The Australo-Malaysian region and the New World tropics are regarded as major centres of bat evolution because of their rich and diverse bat faunas.

## Flight

The ability to fly, the most striking adaptation of bats, was acquired very early in their history. The oldest known bats were already perfectly adapted to flight in having well-developed wings. Nothing is known about how flight evolved, but Jepsen [14] speculated that the hypothetical ancestor may have made short leaps to catch prey with its large, and possibly webbed, front feet. These then evolved into wing-like structures that would sustain the animal in the air for brief periods, and eventually into the refined wings as we know them. The fossil record has thus far not provided any evidence to support the idea.

The wings of bats form thin airfoils that produce both lift and thrust. The proximal part of the wing, between the body and the fifth finger (the plagiopatagium) is convex on top and concave below and produces most of the lift, whereas the movements of the distal segment, from the fifth finger to the edge (the chiropatagium) produce most of the thrust. The camber of

Table 2. The families of bats and their distribution by zoogeographic regions

| | Number of Species[1] | Nearctic | Neotropic | Palearctic | Ethiopian | Oriental | Australasian |
|---|---|---|---|---|---|---|---|
| **Suborder Megachiroptera** | | | | | | | |
| Family Pteropodidae (the flying foxes) | 161 | | | | X | X | X |
| **Suborder Microchiroptera** | | | | | | | |
| Family Rhinopomatidae (the rat-tailed bats) | 3 | | | X | X | X | |
| Family Emballonuridae (the sheath-tailed bats) | 48 | | X | | X | X | X |
| Family Craseonycteridae (the butterfly bats) | 1 | | | | | X | |
| Family Nycteridae (the slit-faced bats) | 14 | | | | X | X | |
| Family Megadermatidae (the false vampire bats) | 5 | | | | X | X | X |
| Family Rhinolophidae[2] (the Old World leaf-nosed bats) | 127 | | | X | X | X | X |
| Family Noctilionidae (the bulldog or fishing bats) | 2 | | X | | | | |
| Family Mormoopidae[3] (the moustached bats) | 8 | X | X | | | | |
| Family Phyllostomidae[4] (the New World leaf-nosed bats) | 139 | X | X | | | | |
| Family Thyropteridae (The New World sucker-footed bats) | 2 | | X | | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Family Furipteridae (the thumbless bats) | 2 | | X | | | | |
| Family Natalidae (the funnel-eared bats) | 4 | | X | | | | |
| Family Vespertilionidae[7] (the plain-nosed bats) | 315 | X | X | X | X | X | X |
| Family Myzopodidae (the Old World sucker-footed bats) | 1 | | | | X[5] | | |
| Family Mystacinidae (the New Zealand short-tailed bats) | 1 | | | | | | X[6] |
| Family Molossidae[7] (the free-tailed bats) | 86 | X | X | X | X | X | X |

[1]based on Honacki et al. 1982
[2]including the Hipposideridae
[3]previously included as a subfamily of the Phyllostomidae referred to as the Chilonycterinae
[4]including the vampire bats, the subfamily Desmodontinae, which is treated as a separate family by some workers
[5]only in Madagascar
[6]only in New Zealand
[7]a family reported in Canada

the wing can be increased by flexing the fifth finger and by lowering the hind leg thus allowing flight at low speed. The power that propels the bat through the air comes from four proximally located muscles, of which the pectoralis muscle is the most important. There are no large muscles in the forearm or fingers, which helps to lighten the wings.

Several types of flight can be distinguished, including flapping flight, glides and hovering. The complex movement of the wings in straight flapping flight is similar to that in birds (Figure 3). The downstroke, which provides the main propulsion, pushes the body up and forward. It begins with the wings raised and extended back slightly behind the centre of gravity of the bat. The wings are then moved down until they are approximately in a horizontal plane. From this plane the wings move obliquely down and forward providing further upward thrust and resistance to forward motion. In the upstroke, which requires less power than the downstroke, the wings are moved up and backwards, resulting in a forward and downward force. During this phase of the wing cycle, the leading edge of the wing is turned up and cuts through the air, thereby reducing the downward pressure. A similar effect is achieved during the latter part of the upstroke by a partial folding of the wing. The tip of the wing describes an approximately elliptical path during a complete cycle. In vespertilionid bats the number of wingbeats varies from 10 to 19 per second depending on the size and speed of the bat. In some species (e.g. *Antrozous pallidus*) flapping flight may be interrupted occasionally by brief glides with fully extended wings. Species that feed on non-flying prey, fruit, pollen or nectar are also able to hover. Hovering flight has been analyzed in detail in the European big-eared bat (*Plecotus auritus*) [21, 23, 24]. The wings beat in a similar pattern to that of flapping flight, but the body is inclined at about 30° to the horizontal with the head raised, and the angle of tilt of the stroke plane to the horizontal is also about 30° (Figure 4), producing just enough thrust to offset the force of gravity. In ordinary flapping flight the body is held more or less horizontal and the angle of tilt of the stroke plane is about 57.8° to the horizontal (Figure 3).

Abrupt turning is achieved by extending and turning the broad side of the flight membrane of the wing in the direction of the turn, while the other wing performs a power stroke (Figure 5). Such turns can be executed very rapidly (1/16 sec.) in small insectivorous species. Gentler turns are produced by a reduction of the braking effect on the side of the turn. Landing is achieved by using the flight membranes to brake (Figure 6), and may be "head-up" (most vespertilionids) or following a somersault, "head-down" (e.g. rhinolophids and *Plecotus*).

Many bats are able to take off from the ground by springing into the air, whereas others, usually more highly specialized for fast direct flight, are unable to do so and require an elevated site from which to launch themselves.

Aside from their primary function in flight, the wings and uropatagium may also be used by aerial feeders in capturing insects (Figure 7). By using its flight membranes, the bat is able to counter the insect's ultimate escape manoeuvres or unintentional erratic flight path. Some bats wrap their wings around their body when resting (e.g. *Rhinolophus*) or use their wings to fan themselves (e.g. *Pteropus*).

Flight styles are related to feeding and roosting habits. Fast-flying species are characterized by long, narrow wings with a reduced surface, resulting from the elongation of the third and fourth fingers and the shortening of

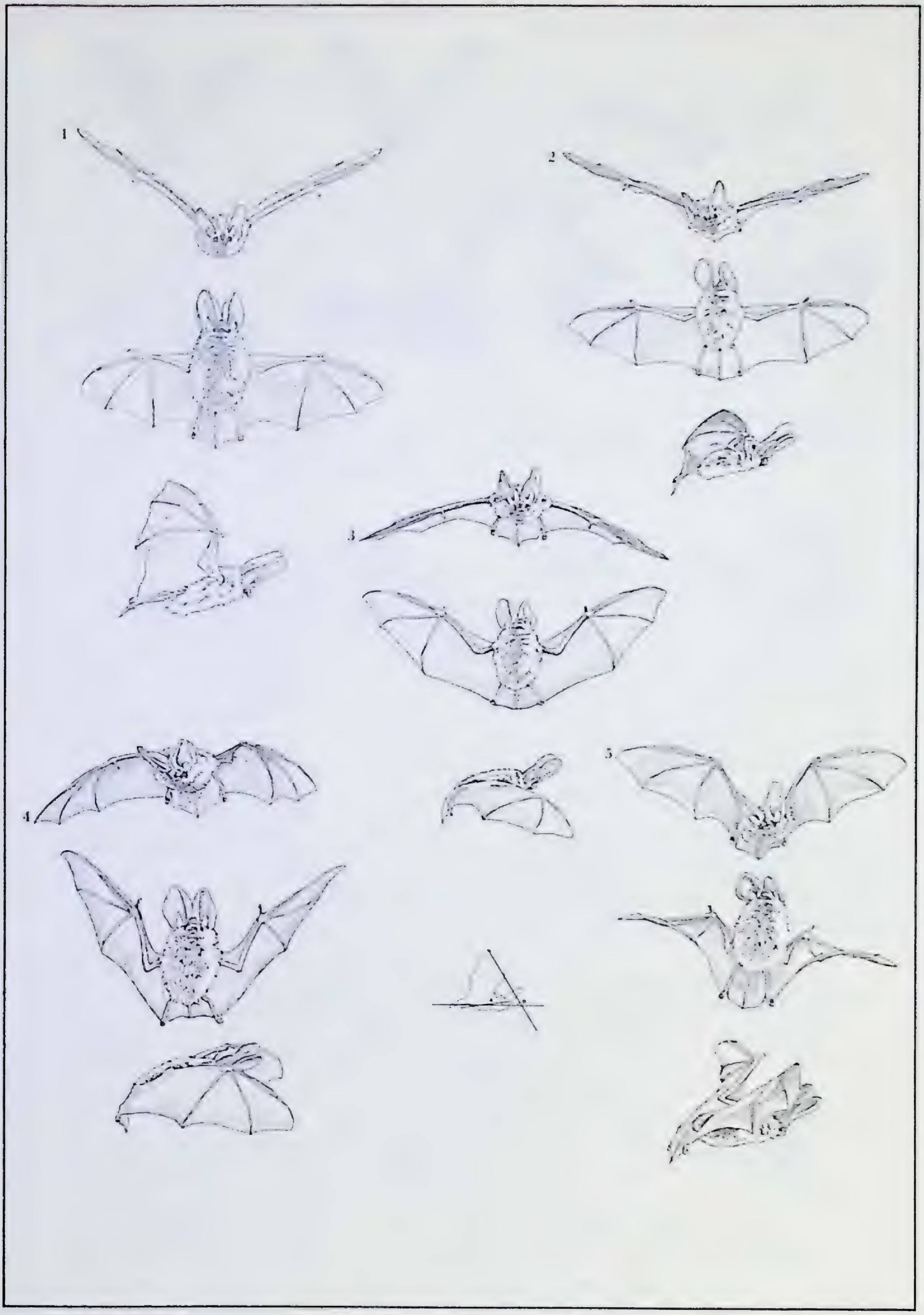



Figure 3. Sequential phases (1–5) of the wing-beat cycle in straight flapping flight of a vespertilionid bat (*Plecotus auritus*) as seen from the front (top), from below (middle) and the side (bottom). The diagram shows the angle of the body and the angle of tilt of the stroke plane to the horizontal in horizontal flapping flight (after Norberg 1976).

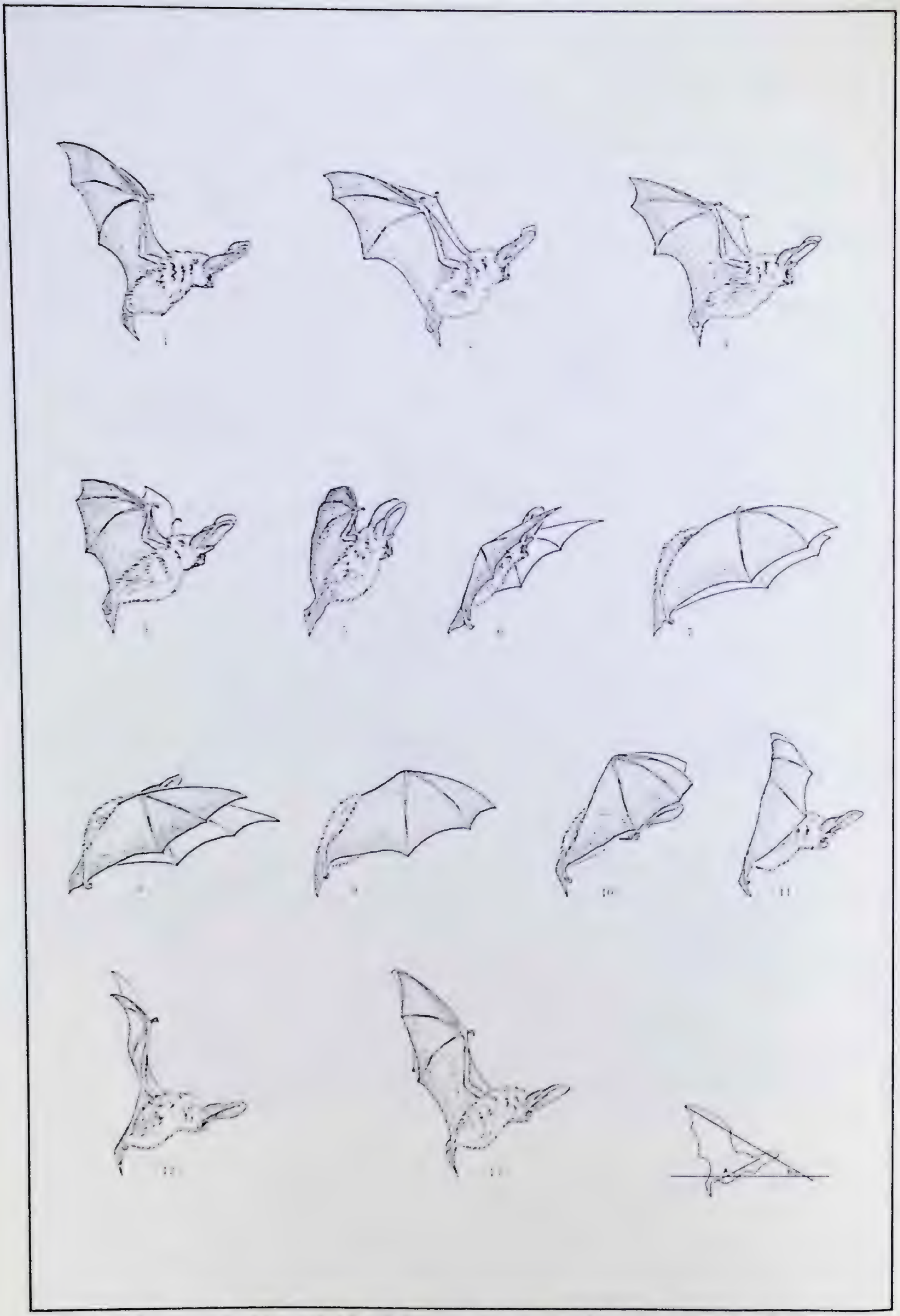


Figure 4. Sequential phases (1–13) of the wing-beat cycle during hovering flight of *Plecotus auritus*. The diagram shows the angle of the body and the angle of tilt of the stroke plane relative to the horizontal (after Norberg 1970).


Figure 5. Sequential position of the wing (a–g) during execution of a turn in *Rhinolophus hipposideros*. The animal, seen from behind at first, is turning right (after Eisentraut 1936).

the fifth finger. Slow-flying, manoeuvrable bats on the other hand have short rounded wings with a relatively large surface area. The aerodynamic characteristic of the wing can be described by the aspect ratio (wing length/breadth) and wing loading (weight/wing area). Wings of high aspect ratio and low wing loading are suited for fast flight in open air, whereas those of low aspect ratio and high wing loading allow low speed manoeuvrable flight near vegetation or the surface of the ground. The difference in the lengths of the third and fifth metacarpal expressed as a percentage of the forearm length can also be used as an index of wing shape and associated flight style.

Flight speeds are difficult to measure in the field, but a few of our native species have been clocked under natural conditions and this gives us a general indication. The eastern pipistrelle flew at an average speed of 18.7 km/h, the larger big brown bat's average speed was 33.3 km/h [20], while a red bat was clocked at 64 km/h in level flight [18].

In many families (Nycteridae, Megadermatidae, Rhinolophidae) there is little locomotion aside from flight. The Pteropodidae move along branches by "walking" upside down suspended by the claws of their feet and sometimes those of the thumbs as well in the manner of a sloth. Rhinopomatids and emballonurids can scramble rapidly in any direction on vertical surfaces using all four limbs. Other bats, including vespertilionids, molossids, noctilionids and vampires crawl well on horizontal and vertical surfaces supported by hind feet, thumbs and thumb pads. A few bats, Thyropteridae, Myzopodidae and some vespertilionids (e.g. *Tylonycteris*) have specialized wrist and sole pads. In the first two families they form disc-like suction cups; in the third they are merely enlarged, permitting the species to move about and roost on smooth surfaces of leaves.

## Echolocation

Closely associated with the evolution of nocturnal flight and the use of caves for roosting and hibernation is the manner in which bats find their way. All Microchiroptera orient chiefly by using the echoes of their own sounds

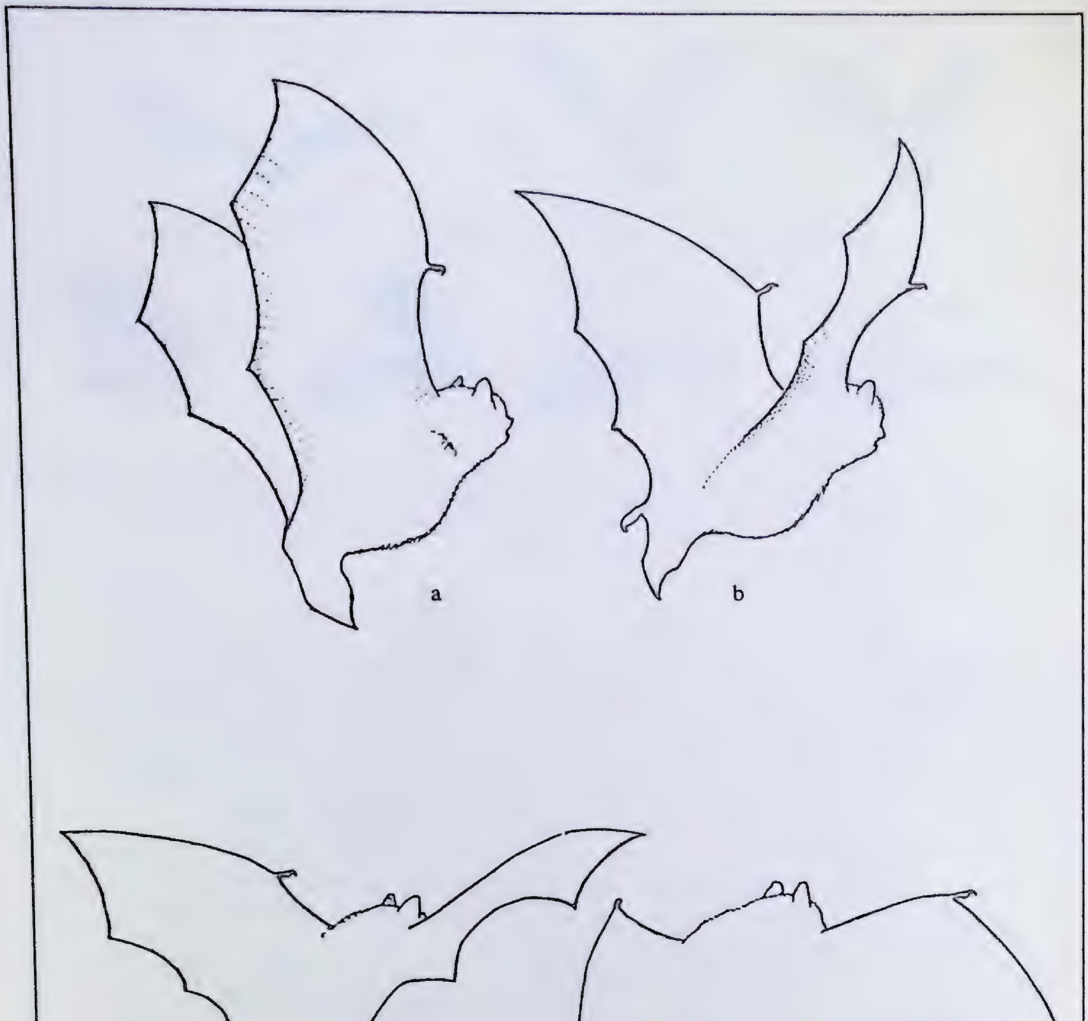


Figure 6. Landing sequence (a–f) (after Gaisler 1964).


Figure 7. Use of flight membranes in capturing insects by *Myotis lucifugus* (after Webster and Griffin 1962). A: use of uropatagium as a net; B: coordinated use of the wing tip and the uropatagium in capturing prey.

(echolocation), whereas the majority of Megachiroptera orient visually. Some cave-dwelling species of the megachiropteran genus *Rousettus*, which independently evolved the capacity to echolocate, are the only exceptions.

Echolocation is accomplished by the emission of short pulses of sound and the subsequent reception of their echoes, reflected by objects in the animal's path. These echoes provide information on direction, distance and velocity, as well as size and nature of these objects. Many bats use echolocation to avoid obstacles as well as to locate, identify and pursue prey. Echolocation sounds may also serve a communicative function. Echolocation has been thoroughly investigated in only a small number of species. In the Microchiroptera the pulses are produced by the vibration of the vocal cords in the larynx and emitted through the mouth or nostrils. In *Rousettus* the pulses are produced with the lips and tongue.

The frequency of the echolocation calls used by bats lies in the high range of the sound spectrum and most are beyond the threshold of human audibility (ultrasonic). Sound of a given frequency has definite physical properties that are important in echolocation. For example, high frequency sound, because of its shorter wave length, would allow a bat to detect smaller targets. On the other hand, high frequency sound undergoes considerable atmospheric attenuation, which limits the effective range. A bat using a high-frequency echolocation call could thus detect smaller prey and get a more detailed mental image of the target than a bat using a lower frequency; on the other hand the distance at which the target could be detected would be smaller. As we shall see, different species of bats have evolved different echolocation calls to suit the particular requirements of their way of life. Aside from echolocation sounds, bats also produce vocalizations that are used in communication and are generally audible to humans.

Facial structures and nose leaves of various shapes and sizes and of differing complexity are present in some families (the Old World Rhinolophidae, Megadermatidae and Nycteridae and the New World Phyllostomidae). These structures may function to channel and beam sound emitted through the nostrils, although experimental evidence for this is still largely lacking. The external ears are generally large and channel incoming sound and aid in determining its direction. It is speculated that the well-developed tragus present in the Vespertilionidae and some other families plays a role in focusing the echoes received. Recent work on *Eptesicus fuscus* [31] shows that in this species the tragus functions to provide the animal resolution in the vertical plane. The inner ear is adapted to high-frequency sound and is acoustically insulated from the rest of the skull, which improves the differential reception of sound signals by both ears. The middle ear is provided with two well-developed small muscles, which are attached to the auditory ossicles. Contraction of these muscles dampens the sound transmission mechanism of the middle ear when loud sound is emitted by the bat, thus preventing the hearing sensitivity from being temporarily impaired by the loudness of the outgoing signal. During the final stages of an attack the incoming echoes are similarly controlled.

The echolocation sounds produced by bats vary, not only from one species to the next, but also in individual bats, to meet the needs of the specific foraging situations. In the course of detection, approach and attack on prey, the echolocation sounds undergo changes in structure, duration, and repetition rate (Figure 8). During the search phase, the duration of individual pulses in most vespertilionids varies from 10 to less than 2 msec

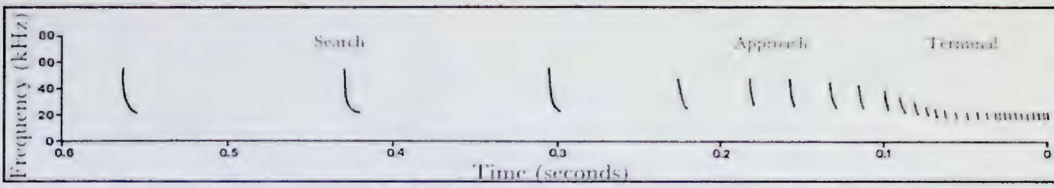



Figure 8. A graphic portrayal of echolocation calls during the (a) search (b) detection and approach (c) terminal phase (feeding buzz) just prior to contact with the prey.

and they are emitted at a rate of 20 to 10 per second. When the bat detects and approaches prey or an obstacle, the pulse duration shortens gradually to a fraction of a millisecond and the repetition rate increases culminating in a rate of 500 calls per second in the final attack. These high pulse repetition rates associated with attacks on flying insects are called feeding buzzes.

Echolocation sounds of different species differ with respect to frequency change over time, duration, number of harmonics, intensity and the number of different types of echolocation calls a species is able to produce (Figure 9 and Table 3). Orientation pulses range in frequency from 8 to 215 kHz and may be divided into two basic types on the basis of their frequency pattern over time. Those that show a change in frequency from beginning to end, usually from high to low, are termed frequency modulated or FM sounds. Those in which a constant frequency is maintained are termed constant frequency or CF sounds. Most species produce echolocation sounds that contain elements of both, although FM or CF components may predominate. One or more harmonics may be present in both types, and increase the precision of the acoustic image of a target the bat obtains. The intensity of the call is the sound pressure level of the signal or the amount of energy in a call. Intensity ranges from 65 dB, in the so-called ''whispering'' bats to over 100 dB in bats feeding on aerial insects. Species that produce high-intensity calls are detectable at a greater distance.

The above characteristics of echolocation calls are functionally related to the interaction of a bat with its prey and may be found in differing combinations in different species exhibiting a range of feeding strategies.

For example a species pursuing its prey in the open is likely to use a narrow band, high-intensity CF pulse, which would allow it to detect its prey at a distance and to gauge its velocity relative to itself by evaluating the Doppler shift of the echoes. Some bats using CF calls, e.g. *Rhinolophus*, are capable of discriminating small Doppler shifts and responding to these by changing the frequency of their emitted CF sounds to keep the frequency of the echo at a value to which the cochlea is sharply tuned (Doppler shift compensation). In this way these bats may reduce the reception of the outgoing pulse, while increasing reception of the incoming echo. The Doppler shift compensation permits the monitoring of small changes associated with insect wingbeats thus enabling bats with this type of echolocation system to detect flying insects easily. The narrow band signal, however, gives little precise information aside from the presence or absence of a target. Species foraging in highly cluttered situations employ broadband FM pulses, which return significantly more information, giving these bats a high resolution acoustic image of their surroundings and allowing them to detect sedentary

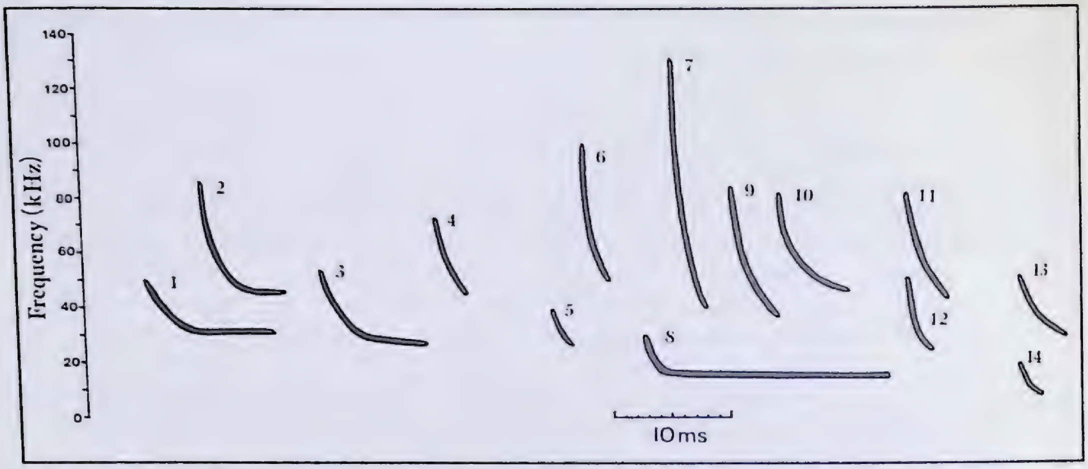



Figure 9. Sound spectrograms of the fundamental search phase echolocation calls of Canadian bats showing frequency change over time. 1) *L. cinereus*; 2) *M. volans*; 3) *E. fuscus*; 4) *P. subflavus*; 5) *P. townsendii*; 6) *M. evotis*; 7) *M. septentrionalis*; 8) *T. macrotis*; 9) *M. lucifigus*; 10) *M. ciliolabrum*; 11) *M. californicus*; 12) *A. pallidus*; 13) *M. thysanodes*; 14) *E. maculatum*.

Table 3. Characteristics of search phase echolocation calls of native species of bats*

| | Highest frequency (kHz) | Lowest frequency (kHz) | Harmonics | Maximum search call duration (ms) |
|---|---|---|---|---|
| 1. *M. lucifugus* | 78 | 38 | 2,3 | 5 |
| 2. *M. volans* | 89 | 40 | 3 | 10 |
| 3. *M. septentrionalis* | 110 | 38 | None | 3 |
| 4. *M. evotis* | 97 | 54 | None | 3 |
| 5. *M. thysanodes* | 49 | 31 | 2 | 8 |
| 6. *M. californicus* | 67 | 37 | 2 | 6 |
| 7. *M. ciliolabrum* | 55 | 41 | None | 5 |
| 8. *P. subflavus* | 73 | 45 | ? | 2,3 |
| 9. *L. borealis* | 97 | 40 | None | 3 |
| 10. *L. cinereus* | 39 | 26 | 2 | 15 |
| 11. *P. townsendii* | 50 | 20 | 2 | 5 |
| 12. *E. maculatum* | 14.5 | 8.6 | 2(3) | 5 |
| 13. *E. fuscus* | 48 | 27 | 3 | 10 |
| 14. *A. pallidus* | 49 | 26 | 2 | 5 |
| 15. *T. macrotis* | 30 | 17 | 2,3 | 20 |

*Data from Fenton and Bell 1981 except: 8 from Griffin 1958; 9 from Webster and Brazier 1968 (cited by Novick in Wimsatt 1977); 11 from Griffin et al. 1963, Grinnell 1963 (cited by Novick in Wimsatt 1977), and Simmons 1980.

prey against a complex background. These pulses also allow the bats to determine distance and direction, as well as the nature of a target. Species that hunt in intermediate situations may employ FM calls with a more or less pronounced CF component.

Other echolocation strategies may have evolved in response to insects, moths in particular, capable of detecting bat echolocation sounds and of taking evasive action to avoid capture. In a number of bats (e.g. *Euderma maculatum* and *Plecotus townsendii*) these strategies involve the use of a combination of frequencies and intensities making these bats less conspicuous to the tympanate moths they hunt. These bats employ frequencies above or below the range to which the moths are acoustically most sensitive, which generally corresponds to the frequencies used by the majority of sympatric bat species in a region. The use of such frequencies in combination with a low or moderate intensity reduces considerably the maximum range at which a moth can detect the bat and increases the chances for a successful pursuit by the bat. Yet another strategy (e.g. that used by *Antrozous pallidus*) involves listening for sound produced by the potential prey.

## Vision and Olfaction

Although the Microchiroptera rely chiefly on their sense of hearing, many have relatively well-developed vision, contrary to popular belief. Vision may be used in a supplementary way by many species and some species locate food primarily by vision. Vision is used to sample light intensity outside the roost and acts as a *Zeitgeber* adjusting circadian and circannual rhythms and probably plays an important role in long distance navigation. The function of the sense of smell is not fully understood. Bats have various exocrine glands, many of which produce distinct scents detectable by humans. It is likely that many of these serve a social or sexual function. Olfaction is also used in finding and selecting food, primarily in fruit, nectar and pollen-feeding bats.

## Roosts

Bats roost in a wide variety of places including trees (cavities, under bark, in foliage), caves, mines, rock crevices and man-made structures (Figure 10). At rest, bats are usually suspended upside down by their hind feet. They may hang free from the ceiling or branch, in contact with the wall, or they may be wedged in narrow crevices. In cold climates with prolonged periods of freezing temperatures, bats select caves and old mines to hibernate. In areas with milder winters some species hibernate in hollow trees, behind loose bark or in similar less insulated sites.

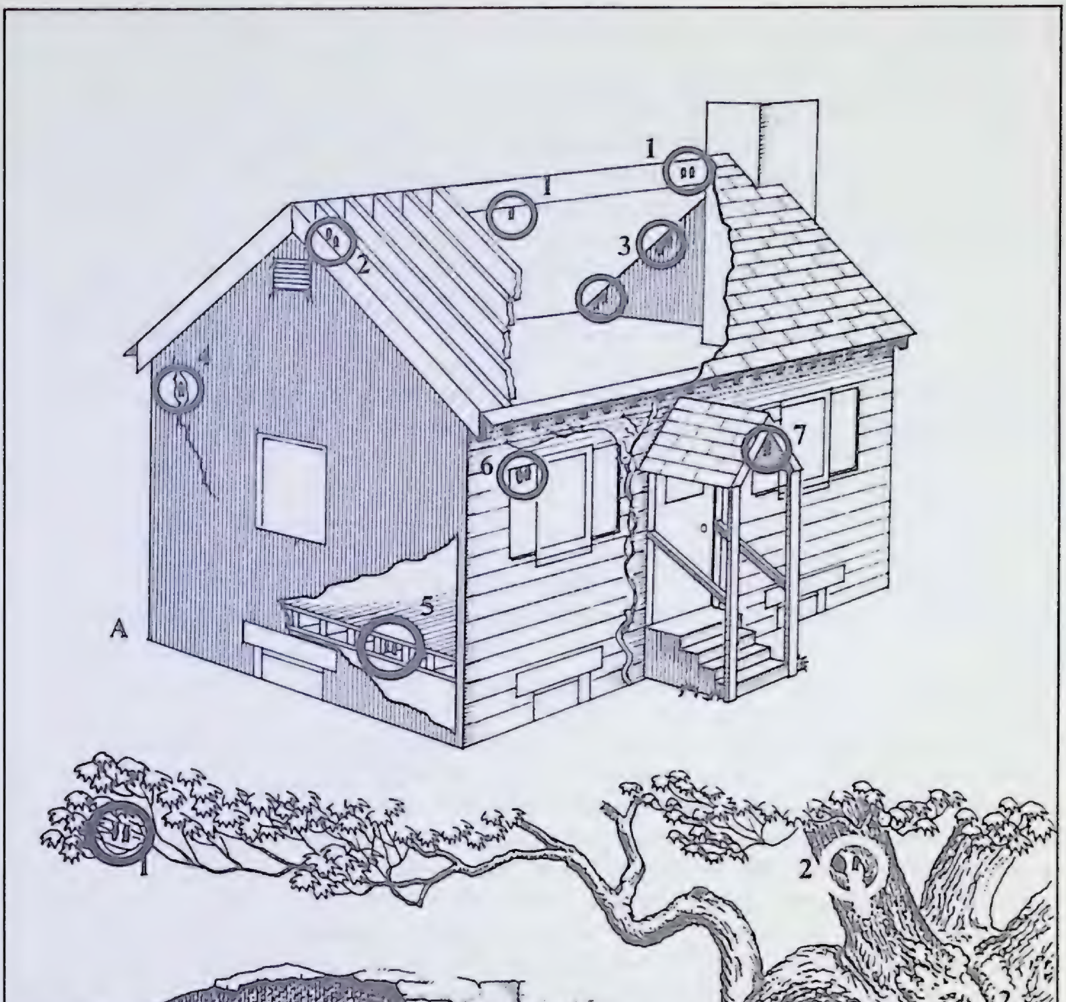
Suspension by the hind feet is made possible by a special mechanism in the toe, which prevents the retractor tendon of the claw from releasing so that a hold can be maintained without the expenditure of muscular energy. The extensor, which has a roughened surface, runs through a sheath with a corrugated inner surface. When the animal's weight pulls on the tendon, the protuberances on the surface of the tendon fit into the corrugations of the sheath and prevent it from slipping back. At the same time a small tendon connecting the phalanx and the sheath exerts an upward pull on the latter, thereby raising the folds in the sheath and securing the hold between it and the tendon. The catch is released when the animal achieves a horizontal position just prior to take-off.

Figure 10. Roosting sites

A. Roosts occupied by bats in houses. In Canada three species use buildings to a h degree: *Myotis lucifugus, M. yumanensis* and *Eptesicus fuscus*. *Plecotus townsendii, M. sep trionalis, M. californicus* and *M. leibii* are occasionally found in buildings. Sites select roosting include (1) main beams and (2) rafters, (3) joints of wall and roof, (4) crac and fissures, (5) spaces in walls and floors, (6) space behind shutters, and (7) porch (used as night roosts).

B. Roosts in trees include (1) twigs or petioles in foliage (*Lasiurus cinereus, L. bore Pipistrellus subflavus?*); (2) Cavities in trunk or main branches (most species of *My E. fuscus* and *Lasionycteris noctivagans*); (3) Crevices and under loose bark (*Myotis* spp. *noctivagans*).

C. Caves and mines are used for hibernation by all Canadian species, except those migrate to milder climes before winter. Some species, such as *Euderma maculatum*, *A zous pallidus* use (1) crevices and fissures in rock faces as summer day roosts, while such as *M. ciliolabrum* may also use (2) spaces in the talus at the foot of cliffs. During hibernation different species select different sites in a cave or mine, near the entrance deep inside, in (3) cracks or crevices in the wall, or (4) hanging free from the ceiling on the wall.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## Migration

Many temperate bats migrate annually between summer roosts and hibernation sites. In the majority of Canadian species, individuals from various localities may travel in different directions, over smaller or greater distances to reach their hibernacula. Species of *Lasiurus* and *Lasionycteris* migrate over long distances in autumn to pass the winter in milder climes and back again in spring.

Seasonal migration may be triggered by some combination of endogenous factors, weather conditions and food availability. We do not know how bats find their way to the hibernacula, which are often hundreds of kilometres from the areas where they spend the summer, nor do we understand how bats learn the location of suitable sites. Navigation from one area to another probably involves vision.

## Thermoregulation

Temperate zone bats, mostly vespertilionids, with some rhinolophids and a few molossids, are heterothermic. These bats may lower their body temperature to ambient temperatures while they are resting during the day (daytime lethargy). Bats belonging to the first two families are also capable of prolonged lethargy characterized by greatly reduced body temperature and metabolic rate during the winter (i.e. hibernation). The advantage of this ability is that the bat can survive unfavourable conditions with a minimum expenditure of energy. Tropical rhinolophids and vespertilionids can also enter torpor during inclement periods. Most tropical bats, however, appear to be homeotherms, that is they react to cooling by increasing their metabolic rate in order to keep their body temperature constant, and they are incapable of hibernation.

Our native species arrive at the hibernacula in autumn or early winter (September–December). Prior to their arrival the bats accumulate body fat to fuel their metabolic processes during hibernation. In autumn 30 per cent of the animal's weight may be fat, all of which will be gone by spring.

Hibernacula are selected on the basis of temperature and humidity, which are strongly influenced by patterns of air flow. The requirements for different species vary; some select cool (e.g. -5 to 0°C), relatively dry situations near the entrance, whereas others select warmer (e.g. 0 to 5°C) and more humid locations. When the temperature of the selected site sinks below a certain critical value, the bat responds by increasing its metabolic rate, raising its body temperature and arousing from torpor. It is then able to move to a more suitable location. Activities such as movement within and sometimes between hibernacula and copulation during the winter are not uncommon. Some species hibernate in clusters, which presumably helps to dampen temperature change and decrease moisture loss while others hibernate singly. Clustering by hibernating bats does not serve to keep the animals warm, unlike clustering in maternity colonies.

## Reproduction

The annual reproductive cycle follows a similar pattern in all our native species. They are monoestrous, mate in autumn and winter and give birth from May to July. Spermatogenesis commences in spring, when testes increase in size, reaches a peak in August, and terminates by the end of the

summer after which testes regress. Viable sperm is stored in the cauda epididymidis throughout the winter and accessory sex organs continue to function. Although the main mating activity takes place in autumn, mating may continue throughout winter. Mounting takes place in a dorso-ventral position and the penis is inserted under the inter-femoral membrane. Coitus lasts for several minutes. Copulation usually takes place while the animals are suspended. Spermatozoa are stored in the uterus. Ovulation and fertilization take place in spring after the females come out of hibernation. The gestation in temperate vespertilionids varies from 7 to 14 weeks; variations in length are imposed by climatic factors.

The females of many species form maternity colonies, usually located in warm sites. The numbers of individuals and selection of warm sites facilitate temperature regulation and promote the rapid growth and development of the young. Most Canadian species have one or two young per litter but *Lasiurus borealis* may have four. The young are large at birth (up to 30 per cent of the mother's weight) but have small wings and well-developed feet and thumbs. Deciduous teeth, some of which are hook-shaped, are present at birth and for a short period thereafter. They apparently assist the neonate in clinging to its mother. The eruption of pemanent dentition is rapid and full adult dentition is present when the young bats are weaned.

## Populations

Populations of temperate bats are generally characterized by relatively low reproductive potential, and by long life, associated with low levels of natural predation. Mortality is highest among juvenile bats during their first winter but relatively low in adults, many of which live to a considerable age. Longevities exceeding 10 years have been recorded in several species. In contrast most other small mammals of similar size rarely survive beyond two or three years. Little is known about the major causes of mortality. Accidents may be an important mortality factor. Human interference at hibernacula, use of pesticides, destruction of roosts and direct extermination are considered to be responsible for the decline in a number of species in North America and Europe, some of which are now listed as threatened or endangered.

## Parasites

Bats are often infested with ectoparasites. The ears and wing membranes harbour small mites, while fleas, ticks and bat flies may be found in the fur. The bat flies are highly specialized Diptera of the families Streblidae and Nycteribiidae, which are restricted to bats. In the roosts, bat bugs (Cimicidae) are often common. Of the endoparasites, intestinal helminths and protozoan have been reported. A detailed overview of the parasites of bats found in Canada is not possible at present, as the basic information is not available.

## Food

The Chiroptera display a remarkable diversity of feeding adaptations. The majority are insectivorous, but some are piscivorous (e.g. *Noctilio leporinus*, *Myotis (Pizonyx) vivesi)*, several are carnivorous (some Phyllostomidae and Megadermatidae), and a few feed only on blood (Desmodontinae). Most

Megachiroptera and many Phyllostomidae eat fruit, while some (Macroglossinae, Glossophaginae) feed at least partly on nectar and pollen.

All species of bats native to Canada are insectivorous and lack striking feeding specializations. Studies of food habits, morphology and foraging behaviour, however, reveal that our native species show some trophic specialization, while retaining a degree of flexibility and opportunism. On the basis of feeding behaviour, two trophic categories are represented in our bat fauna: aerial foragers (most of our bats) and gleaners (*Antrozous* and long-eared *Myotis*). Aerial foragers capture insects in the air, whereas gleaners take their prey from the ground or foliage. The two categories are not necessarily exclusive and overlap in many species, with some aerial foragers occasionally gleaning and, vice versa, gleaners capturing insects in the air.

How, or indeed whether or not, sympatric insectivorous bats partition food resources is not fully understood at present. The morphological and behavioural characteristics related to feeding and the possible basis for partitioning of resources include size, wing shape, shape and size of ears (Figure 1), cranial and dental characteristics, flight style, type of echolocation used, and where and when a bat hunts. All these factors differ to a greater or lesser degree from one species to the next and combine to form different, although, in some species, overlapping trophic niches. Taking a closer look at some of these factors, one can see how they might operate singly or in combinations to achieve a differential exploitation of the available food resource. Small bats tend to feed on smaller prey than large bats. Wing shape and flight style, as well as type of echolocation call used and ear morphology, are related to where and how a bat most efficiently can search, detect, pursue and capture its prey. Species with massive rostra and mandibles, robust teeth and well-developed lambdoidal and sagittal crests for the attachment of strong jaw muscles are capable of preying on hard prey (beetles), whereas those with slender rostra and mandibles, weaker teeth and smooth globular crania hunt soft-bodied insects. As to the behavioural aspects of foraging, the time and place a species hunts will influence the types of insects taken. Further details on this may be found in individual species accounts. A trophic ordination of Canadian vespertilionids based on several morphological characters related to the manner of hunting and feeding is given in Figure 11.

## Conservation

Bats have probably suffered less from direct human persecution than most other mammals because of their nocturnal volant way of life and their hidden daytime roosts. Man-made structures, by providing suitable roosts, probably have had a positive influence on the distribution and abundance of many species of bats. However, because of recent changes in building methods, weather sealing and insulation standards, new buildings provide fewer opportunities for roosting than older buildings.

Increased interest in speleology and increased numbers of visitors to caves have had a deleterious effect on bat populations. Temperate cave-dwelling species are particularly susceptible to disturbance during hibernation. Many caves have been abandoned by bats because of human disturbance. Banding has been in part responsible for the decline of a number of bats by increasing mortality through mechanical damage, infection, decreased mobility and prolonged disturbance during hibernation. In addition to disturbance and

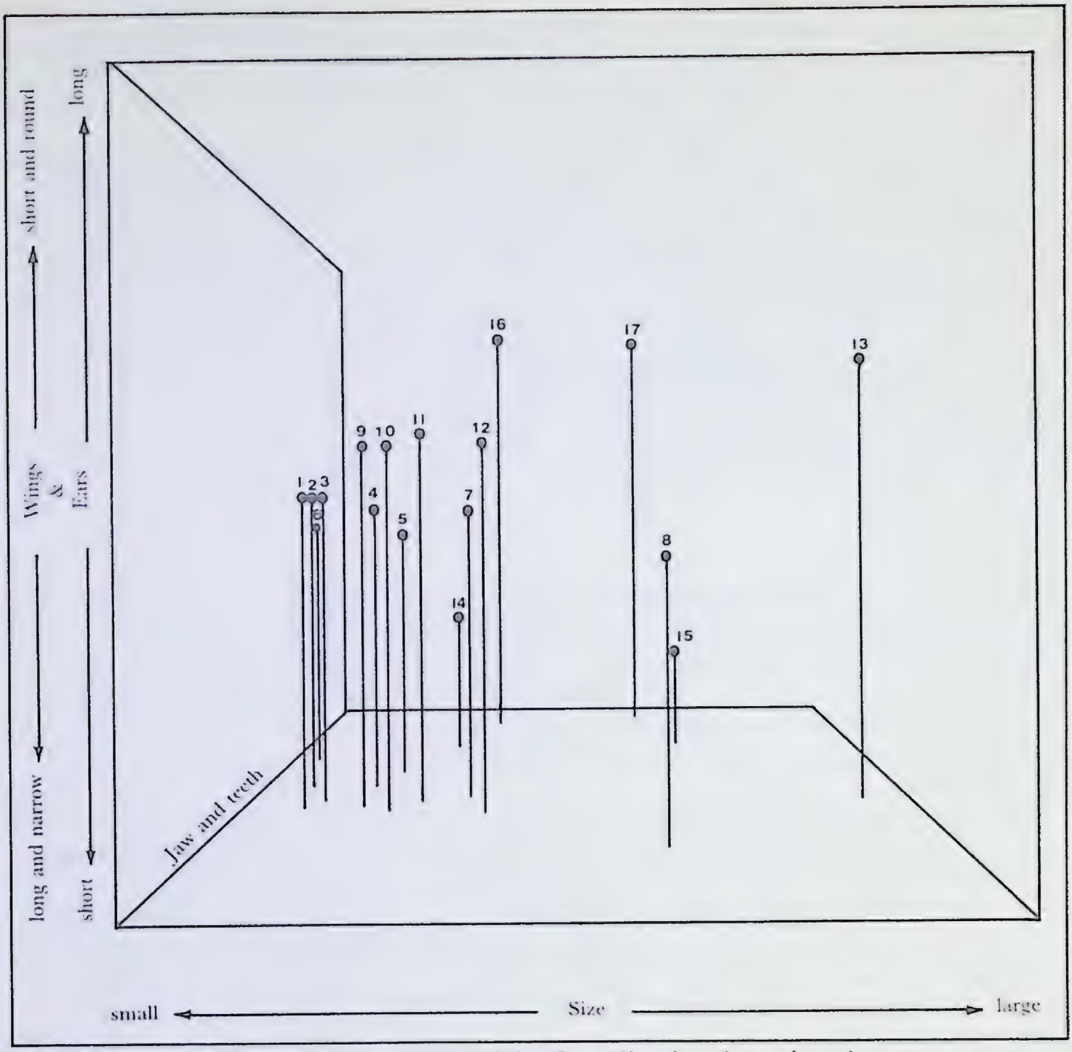


Figure 11. Ecomorphological structure of the Canadian bat fauna based on seven morphological characters related to feeding. The horizontal axis separates the species on the basis of size, with the smallest species on the left, the largest to the right. The vertical axis ranks the species on the basis of wing shape and size of ears, those with long narrow wings and short ears are placed low in the three-dimensional space, those with long ears and shorter and broader wings high. The third axis indicates the degree of robustness of the teeth and jaws. The species nearest the front have relatively more robust teeth and heavier jaws than those in the back. The majority of species resemble each other closely with a few species being more remote. Morphologically similar species may share the same environment by behavioural and ecological differentiation as well. See text. 1) *M. californicus*; 2) *M. ciliolabrum*; 3) *M. yumanensis*; 4) *M. lucifugus*; 5) *M. volans*; 6) *P. subflavus*; 7) *L. noctivagans*; 8) *E. fuscus*; 9) *M. keenii*; 10) *M. septentrionalis*; 11) *M. evotis*; 12) *M. thysanodes*; 13) *A. pallidus*; 14) *L. borealis*; 15) *L. cinereus*; 16) *P. townsendii*; 17) *E. maculatum*.

the loss of roosts and hibernacula, the general use of insecticides has been destructive through direct contact in applications specifically made to exterminate bats from buildings and through accumulation of the poison in the bat's tissues through the food chain.

Effective conservation of bats can be achieved by the protection of hibernacula, maternity roosts, prevention of the general degradation of summer foraging habitats and through public education.

When control is necessary, those measures that are most effective and least harmful to the bats should be selected. The most effective way to keep bats out of a building is to locate and seal the entrance through which bats come and go. Holes as small as 5 mm across should be blocked by using screen, caulking or molding. The sealing should be done when the bats are not in. The best time for this is early (April) or late in the season (October, November). If blocking is not possible, lighting an attic can deter bats, but the light must be left on all the time.

**Public Health**

In some parts of the world, bats pose a public health problem because of their involvement in the direct and indirect transmission of rabies and histoplasmosis. This is not the case in Canada. Rabies, a viral disease of the central nervous system, is transmitted through the bite of an infected mammal or by an aerosol route in caves with conditions of high humidity and temperature such as are found in the subtropical and tropical parts of the continent.

The epidemiology of rabies in bats is not understood and there appears to be no obvious connection with rabies in carnivores. The incidence of the disease in Canadian bats is low compared to that in native carnivores (foxes, skunks) and only a few species (big brown, hoary and pallid bat) are large and powerful enough to break the skin when handled. It is therefore advisable to wear gloves when handling these bats. Any animal exhibiting abnormal behaviour should be avoided and any bites should receive immediate medical attention.

Histoplasmosis is a fungus disease affecting the lungs, with symptoms similar to tuberculosis. The fungus and its spores are associated with bird and bat droppings. Inhalation of airborne spores is the usual route of infection. In Canada most cases of histoplasmosis can be linked to pigeon and chicken droppings, whereas bat droppings are not known to harbour the fungus here.

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*Vision and Olfaction*
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*Populations*
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*Parasites*
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*Food*
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*Conservation and Control*
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*Public Health*
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# Key to the Chiroptera of Canada

## A Using External Characters

This key is designed to identify whole adult specimens in the hand. A millimetre ruler and, in some cases, a hand lens are required. Subadults or young of the year usually show the diagnostic characters of the adult, but may differ in colour. Young bats can be distinguished from adults by their darker pelage (in July) and, until early autumn, by the unossified epiphyses at the metacarpal-phalangeal joints (Figure 12). Adult males can be distinguished by the presence of a conspicuous penis. During the period of active spermatogenesis, enlarged testes are also obvious. Adult females usually have worn fur around the nipples, which are on the side of the chest in an almost axillary position. Non-volant young cannot be identified using this key; their identification has to be based on that of the associated adults. After a tentative identification has been arrived at using the key, the specimen should then be compared with the description given in the species account and the corresponding distribution map should be consulted.

Careful examination usually results in quick and correct identification of most Canadian bats. However, it is easy to confuse several pairs of species. For example, *Myotis evotis* with a well-developed fringe on the uropatagium can sometimes easily be mistaken for *Myotis thysanodes*, unless careful attention is paid to relative size of the ears. The similar *Myotis ciliolabrum* and *Myotis californicus* occur together in the Okanagan Valley but can usually be separated by the shape of the naked part of the snout and the colour of the pelage. The external diagnostic characters given for *Myotis lucifugus* and *Myotis yumanensis* may not serve to separate all specimens in some parts of southern British Columbia, a reflection of the morphological convergence of these bats in this area. The remarks under Similar Species in each species account list the species that may be confused with the species being discussed and should alert the reader to possible difficulties in making identifications. In cases where there is doubt about the identity of a bat, a voucher specimen should be prepared if possible and submitted to an expert.

Since *Myotis sodalis* occurs in northern New York State and may range into southern Ontario, it has been included in the key.

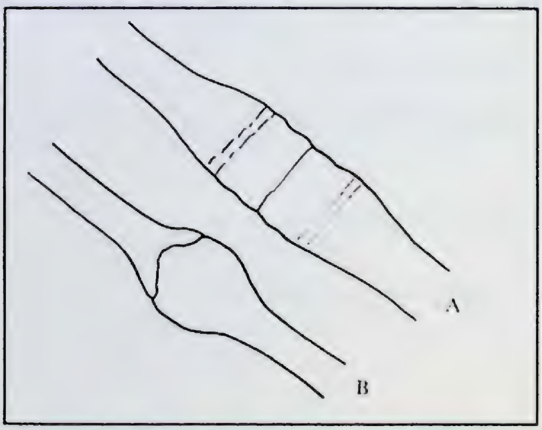


Figure 12. Metacarpal-phalangeal joint in (a) juvenile and (b) adult bat.

1. Approximately half of the tail protruding beyond the posterior edge of the uropatagium; lips wrinkled (Figure 13a) . . . . . . . . . . . . . . . . . . . . . . . . . . . *Tadarida macrotis*, p. 181

Tail virtually completely enclosed by uropatagium; lips not wrinkled (Figure 13b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

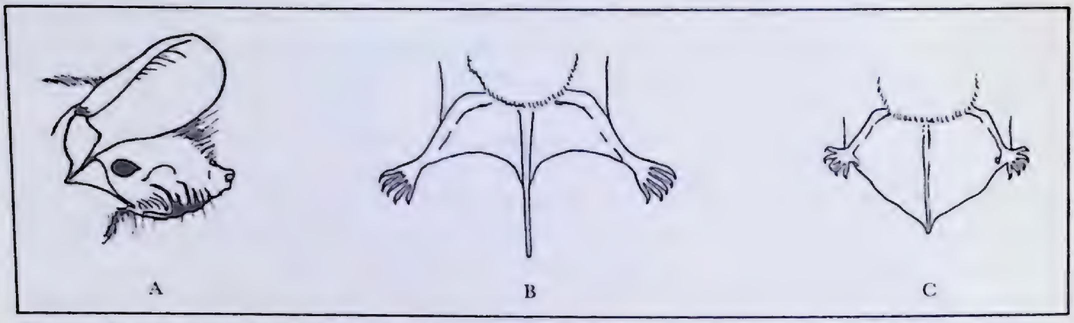


Figure 13. Face and tail of *Tadarida macrotis* (a and b) and tail of a vespertilionid bat (c).

2(1) Ears large, usually more than 28 mm from notch to tip . . . . . . . . . 3

Ears small, less than 28 mm from notch to tip . . . . . . . . . . . . . . . . 5

3(2) Dorsal fur black with two large white spots (approximately 1.5 cm in diameter) near the shoulders and one large white spot on the rump . . . . . . . . . . . *Euderma maculatum*, p. 153

Dorsal fur not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4(3) Fur brownish, dark at base; prominent lumps on either side of the snout . . . . . . . . . . . . . . . . . . . . . . *Plecotus townsendii*, p. 147

Fur pale, yellowish, light at base; no prominent lumps on snout . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Antrozous pallidus*, p. 172

5(2) Fur blackish or dark chocolate-brown with many white-tipped hairs . . . . . . . . . . . . . . . . . . . . . . *Lasionycteris noctivagans*, p. 128

Fur not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6(5) Dorsal side of the uropatagium densely furred . . . . . . . . . . . . . . . . . 7

Dorsal side of the uropatagium naked or sparsely furred basally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

7(6) Rounded ears edged with black; fur a mixture of yellowish, dark brown and white . . . . . . . . . . *Lasiurus cinereus*, p. 140

Rounded ears pale in colour not edged with black; fur red or orange grey . . . . . . . . . . . . . . . . . . . . . . *Lasiurus borealis*, p. 134

8(6) Upper canine in contact with large premolar (P4), 1/2 as high as canine (Figure 14a) . . . . . . . . . . . . . . . . 9

Upper canine separated from large premolar (P4) by one or two small premolars, less than 1/3 as high as the canine (Figure 14b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

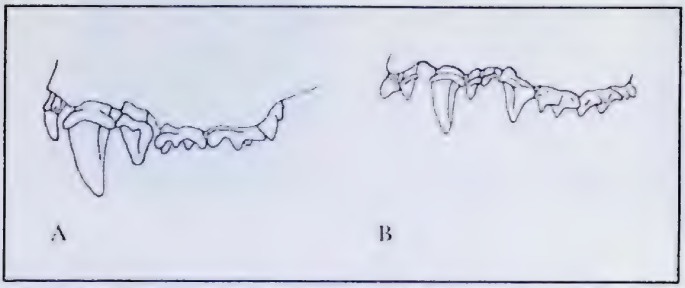
Figure 14. Upper tooth row of (a) *Eptesicus* and (b) *Myotis*.

9(8) Larger; FA 42-51 . . . . . . . . . . . . . . . . . . . . . . . . *Eptesicus fuscus*, p. 160

Smaller; FA 33-39 . . . . . . . . . . . . . . . . . . . . *Nycticeius humeralis*, p. 167

10(8) One small premolar between upper canine and P4 (Figure 15a); fur on back, when parted, shows dark band at the base, yellowish-brown band in the middle, and dark brown tips (Figure 16a) . . . . . . . *Pipistrellus subflavus*, p. 122

Two small premolars between upper canine and P4 (Figure 15b); fur on back, when parted, not as above, usually showing two colours, blackish at base, brown at the tips (Figure 16b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

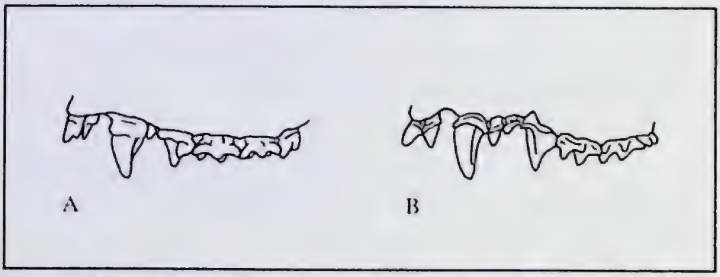
Figure 15. Upper tooth row of (a) *Pipistrellus* and (b) *Myotis*.

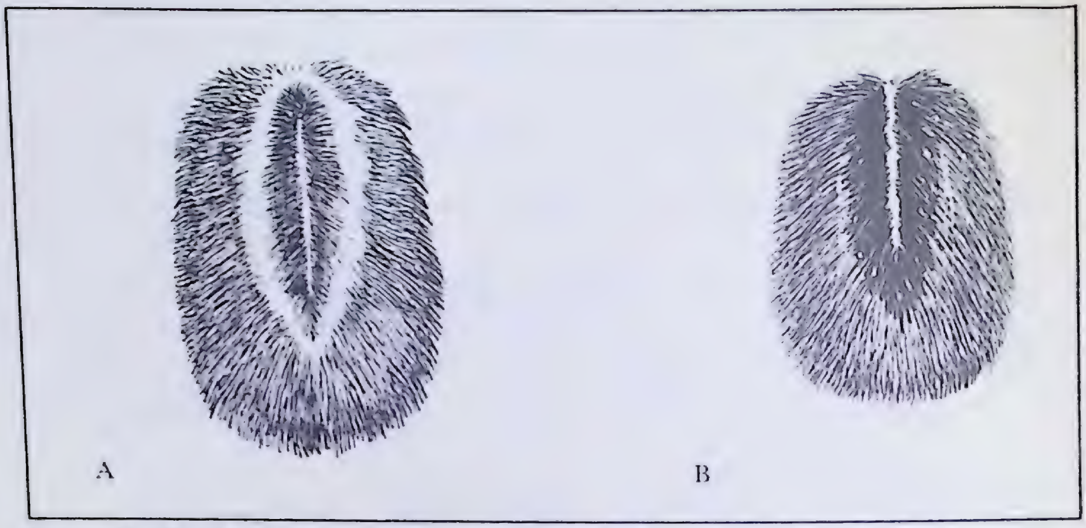


Figure 16. Bands of colour in the parted fur of (a) *Pipistrellus* and (b) *Myotis*.

11(10) Ears relatively long, when laid forward extending well beyond the tip of the nose . . . . . . . . . . 12

Ears short, when laid forward not extending beyond the tip of the nose . . . . . . . . . . 18

12(11) Hind foot small, less than 8 mm . . . . . . . . . . 13

Hind foot large, more than 8 mm . . . . . . . . . . 15

13(12) Pelage glossy brown, eastern . . . . . . . . . . *Myotis leibii*, p. 116

Pelage not glossy, flaxen or yellowish brown to brown, western . . . . . . . . . . 14

14(13) Colour chestnut to dark brown, hair on face brown; naked part of snout about as long as the width of the nostrils when viewed from above (Figure 17a) . . . . . . . . . . *Myotis californicus*, p. 106

Colour flaxen or yellowish brown, usually with contrasting black hair on face; naked part of snout approximately 1½ times the width of the nostrils (Figure 17b) . . . . . . . . . . *Myotis ciliolabrum* p. 111

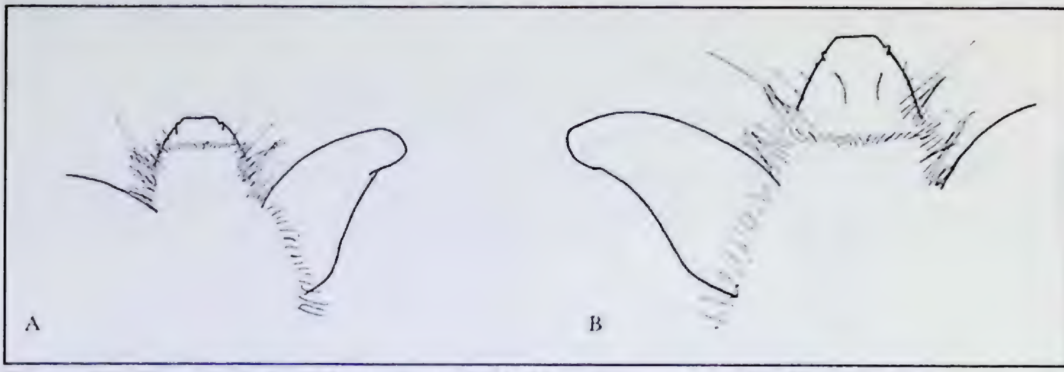


Figure 17. Dorsal view of the snouts of (a) *M. californicus* and (b) *M. ciliolabrum*.

15(12) FA > 40; ear less than half the length of the forearm; conspicuous fringe of stiff hairs on the free edge of the uropatagium (Figure 18) . . . . . . . . . . . . . . . *Myotis thysanodes*, p. 101

FA < 40; ear longer than half the length of the forearm; no conspicuous fringe on the free edge of the uropatagium . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

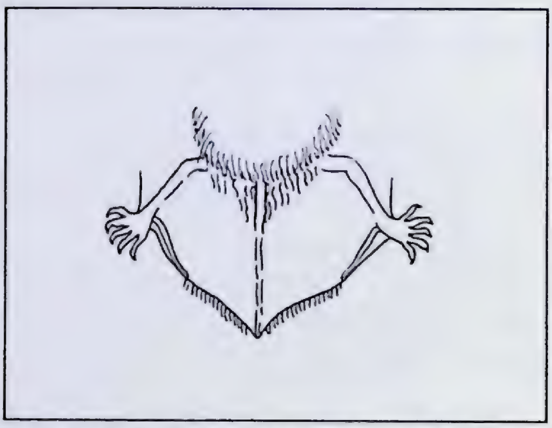

Figure 18. Fringe on the free edge of the uropatagium of *M. thysanodes*.

16(15) Ears black and extending more than 5 mm beyond the tip of the nose when laid forward . . . . . . . . . . . . . . *Myotis evotis*, p. 96

Ears dark, but not black, and extending less than 5 mm beyond the tip of the nose when laid forward . . . . . . . . . . . . . . . . . 17

17(16) Ill-defined dark spot at shoulder and scattered hairs on free edge of uropatagium (use hand lens) . . . . . . . *Myotis keenii*, p. 87

No dark spot at shoulder and free edge of uropatagium usually bare or with only few scattered hairs (less than 20 on one side) . . . . . . . . . . . . . . . . . . . . . . . . *Myotis septentrionalis*, p. 91

18(11) Calcar keeled (Figure 19a) .................................... 19

Calcar not keeled (Figure 19b) ................................ 20

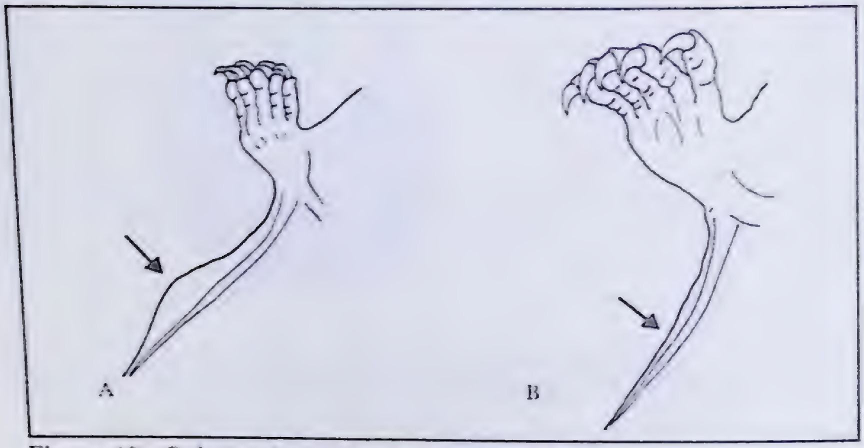


Figure 19. Calcar (a) with and (b) without keel.

19(18) Tibia more than 18 mm; foot less than 45 per cent of the length of the tibia; western .................. *Myotis volans*, p. 83

Tibia less than 17 mm; foot more than 45 per cent of the length of the tibia; eastern ...................... *Myotis sodalis* *

20(18) Dorsal fur long and glossy, basal fur on shoulders usually dark and showing; ears dark brown to blackish; FA 34-40 ...................................... *Myotis lucifugus*, p. 68

Dorsal fur short and dull, dark basal fur on shoulder usually lacking, ears paler; FA 32-38 ...... *Myotis yumanensis*, p. 78

(N.B. In southern British Columbia, where these two species are sympatric, these characters may not allow identification of all individuals.)

* See comment on p. 49

## B Using Cranial Characters

For the identification of skulls, in particular the small ones, a binocular dissecting microscope with ocular micrometer and dial caliper capable of measuring to the nearest 0.1 mm are required. For the critical identification of skulls of similar species (*M. evotis*, *M. septentrionalis* and *M. keenii*; *M. volans*, *M. lucifugus* and *M. yumanensis* and bats of the *M. leibii* group) see Appendix I.

1 Skull large (SL 22–24); gap between the premaxilla narrow (Figure 20a), less than the width of the canine; outlines of interorbital area parallel; lower incisors bifid . . . . . . . . . . *Tadarida macrotis*, p. 181

Skull smaller (SL < 22); gap between the premaxillae wide (Figure 20b), greater than the width of the canine; outline of interorbital area not as above; lower incisors trifid . . . . . . . . . . 2

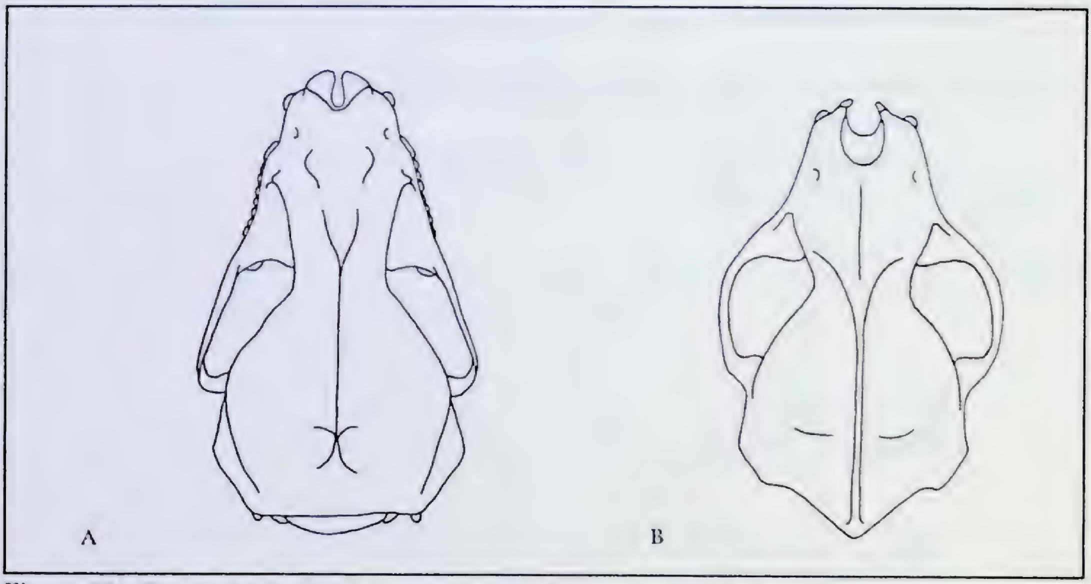

Figure 20. Dorsal view of (a) molossid and (b) vespertilionid skull.

2(1) Number of lower incisors 4 . . . . . . . . . . *Antrozous pallidus*, p. 172

Number of lower incisors 6 . . . . . . . . . . 3

3(2) Number of upper incisors 2 . . . . . . . . . . 4

Number of upper incisors 4 . . . . . . . . . . 6

4(3) Upper incisor distinctly separated from canine; one upper premolar on each side . . . . . . . . . . . *Nycticeius humeralis*, p. 167

Upper incisor touching canine; two upper premolars, the first minute and situated at the base of the canine (Figure 44) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5(4) SL > 16 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Lasiurus cinereus*, p. 140

SL < 15 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Lasiurus borealis*, p. 134

6(3) One upper premolar present on each side; skull large (SL > 17) and broad (MW > 9) . . . . . . . . . . . . *Eptesicus fuscus*, p. 160

More than one upper premolar present on each side; skull smaller (SL < 17) and not as broad (MW < 9) . . . . . . . . . . . . . 7

7(6) Two upper premolars present on each side . . . . . . . . . . . . . . . . . . . . 8

Three upper premolars present on each side . . . . . . . . . . . . . . . . . 11

8(7) Skull larger (SL > 14) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

Skull smaller (SL < 14) . . . . . . . . . . . . . . . *Pipistrellus subflavus*, p. 122

9(8) Skull slender, profile of top of skull highly arched (Figure 21a); narrow rostrum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

Skull broad, profile of top of skull flattened (Figure 21b); broad rostrum . . . . . . . . . . . . . . . *Lasionycteris noctivagans*, p. 128

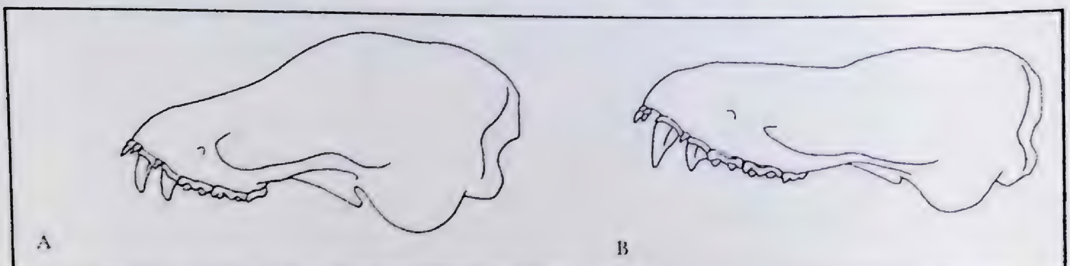


Figure 21. Profile of the skulls of (a) *Plecotus* and (b) *Lasionycteris*.

10(9) SL < 18; three lower premolars . . . . . . . . . . *Plecotus townsendii*, p. 147

SL > 18; two lower premolars . . . . . . . . . . *Euderma maculatum*, p. 153

11(7) IOW < 3.4 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

IOW > 3.4 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

12(11) Frontal area of cranium forming a steep slope relative to rostrum (Figure 22a); covariation of cranial depth and coronoid height falling below line in Figure 23 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *M. californicus**, p. 106

Frontal area of cranium forming a gradual slope relative to rostrum (Figure 22b); covariation of cranial depth and coronoid height falling above line in Figure 23 . . . . . . . . . . . . . . . . 13

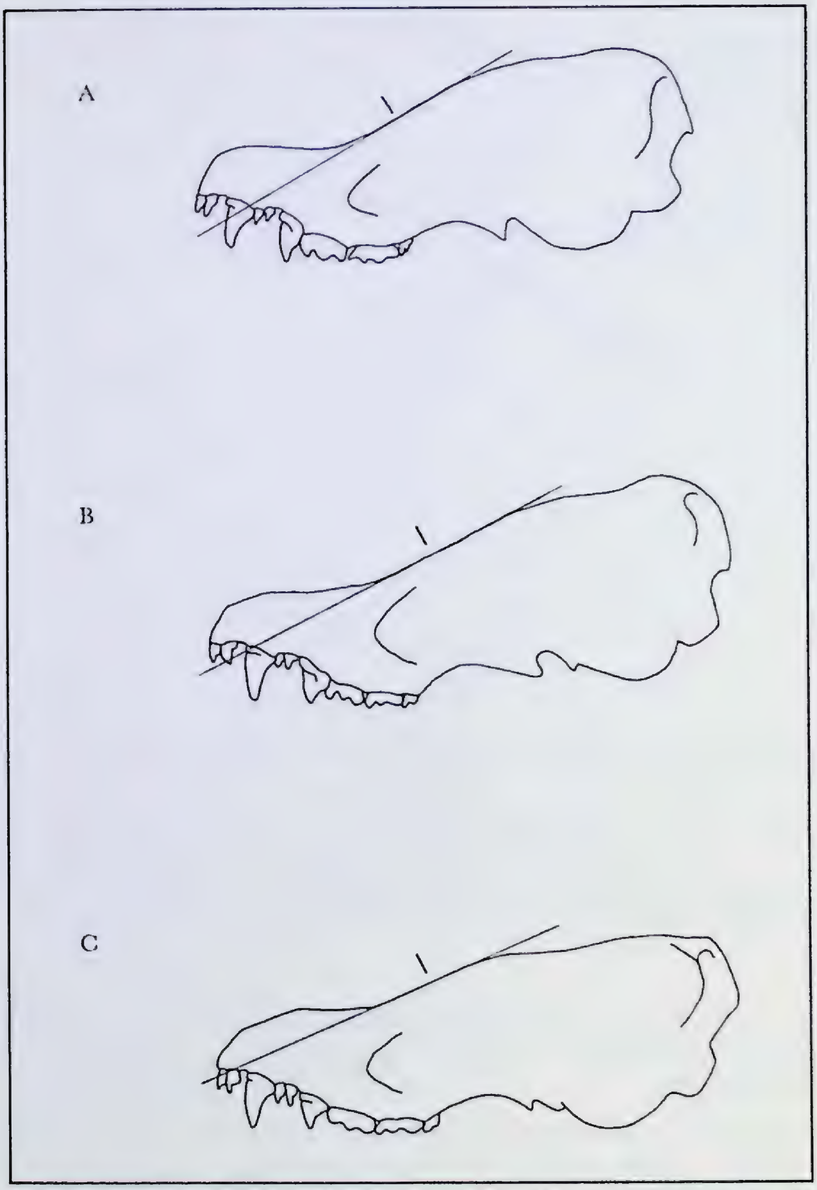


Figure 22. Profile of the skulls of (a) *M. californicus*, tangent at cribriform plate (location indicated by line at right angle to tangent) intersects alveolar line at the canine, (b and c) other species in the *leibii* group, tangent at cribriform plate intersects alveolar line anterior to canine.

*For critical identification of skulls of small-footed bats of the *leibii* group, see Appendix, part A.

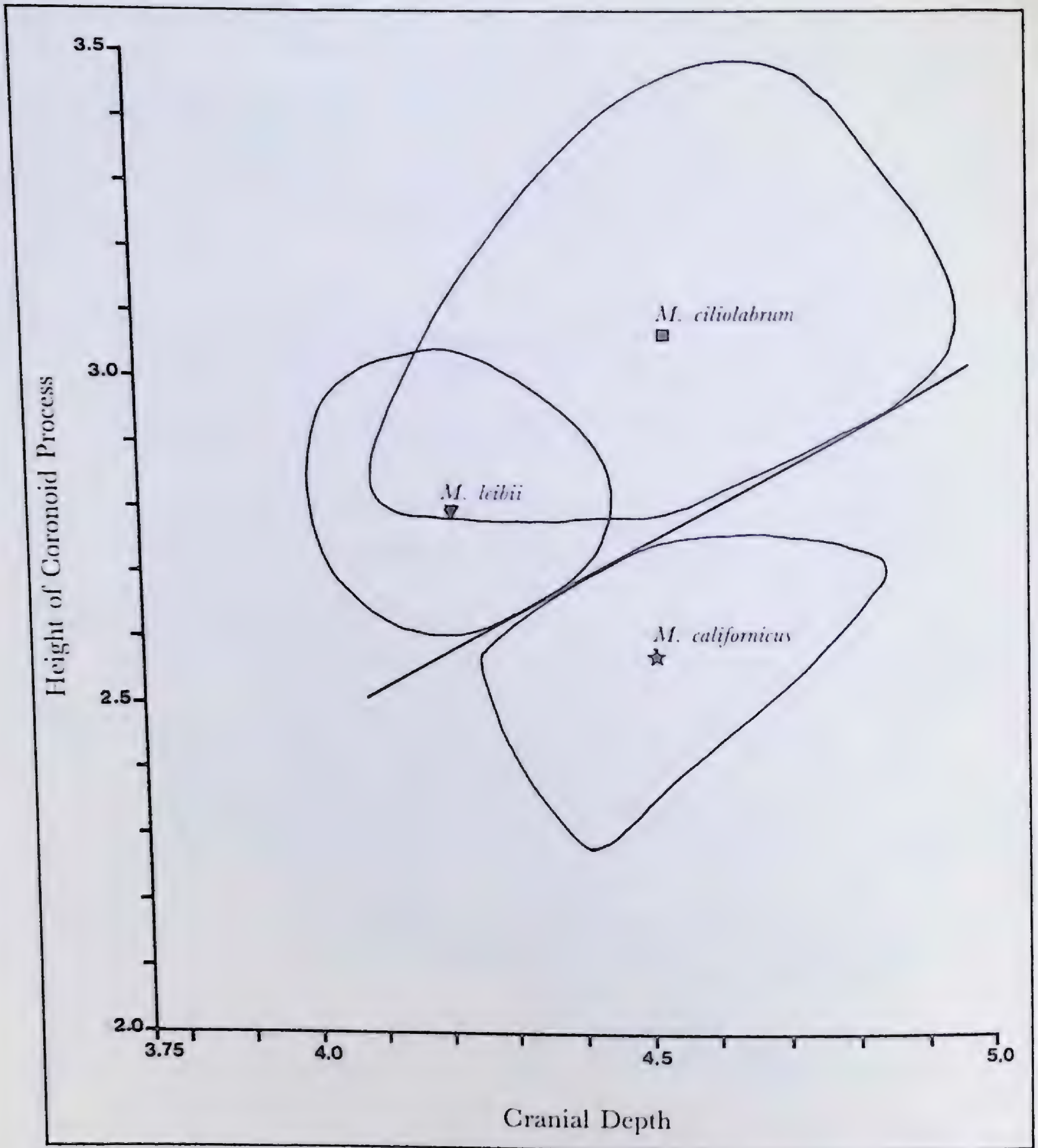

Figure 23. Covariation of cranial depth (CD) and height of the coronoid process in bats of the *leibii* group.

13(12) Roof of braincase covering cerebellar fossa very flat dorsally (Figure 24a); covariation of P4M3L and I3I3W above line in Figure 25 . . . . . . . . . . . . . . . . . . . . *Myotis leibii**, p. 116

Roof of braincase covering cerebellar fossa domed Figure 24b; covariation of P4M3L and I3I3W below line in Figure 25 . . . . . . . . . . . . . . . . . . . . . . . . . . *Myotis ciliolabrum**, p. 111

*For critical identification of skulls of small-footed bats of the *leibii* group, see Appendix, part A.

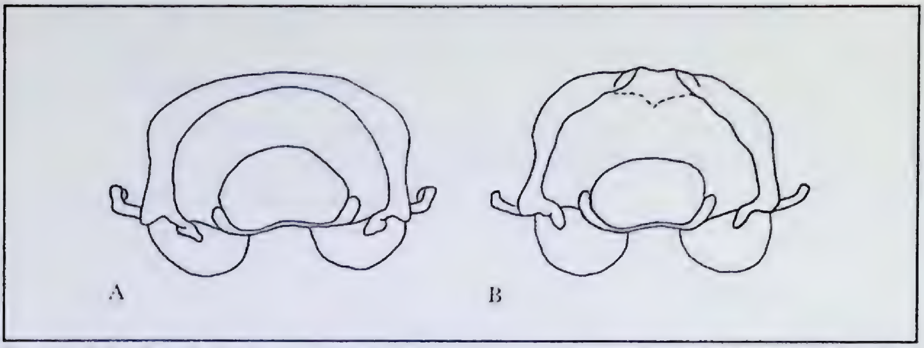


Figure 24. Roof of the cerebellar fossa in posterior aspect (a) *M. leibii* and (b) *M. ciliolabrum*.

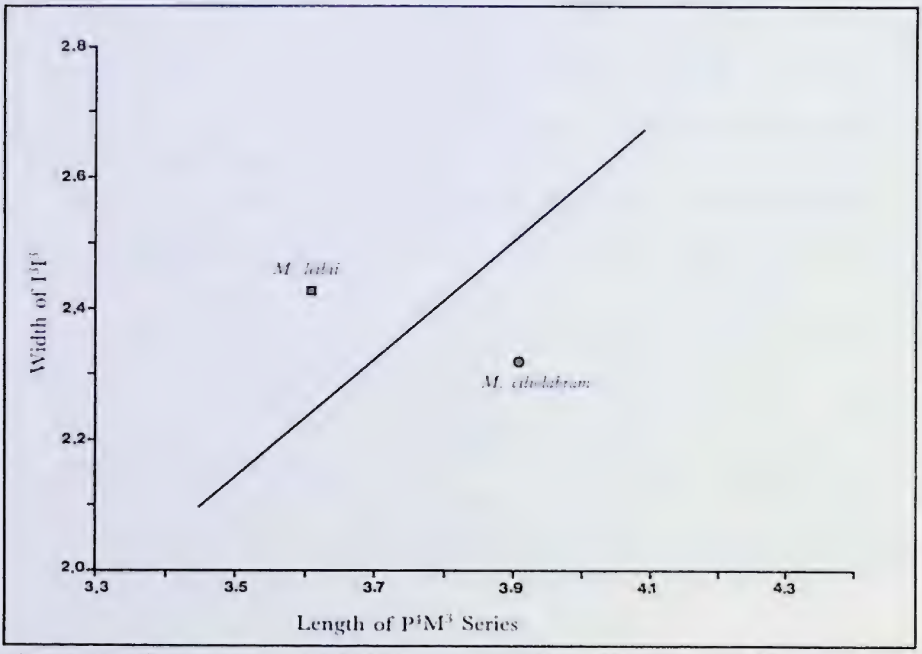


Figure 25. Covariation of P4M3L and I3I3W in *M. leibii* and *M. ciliolabrum*.

14(11) The ratio IOW/MTL<0.70 .......... 15
The ratio IOW/MTL>0.70 .......... 18

15(14) P4M3L>4.2 .......... 16
P4M3L<4.2 .......... 17

16(15) M3M3W>6.2; M3M3W>MTL .......... *Myotis thysanodes*, p. 101
M3M3W<6.2; M3M3W<MTL .......... *Myotis evotis**, p. 96

*If specimen originates from area where *M. keenii* or *M. septentrionalis* occur, see Appendix, part B.

17(15) Profile of frontal area of cranium sloping gradually (Figure 26a); width of canine at cingulum >0.76 ........................................ *Myotis septentrionalis*, p. 91

Profile of frontal area of cranium sloping more steeply (Figure 26b); width of canine at cingulum <0.76 ........................................ *Myotis keenii*, p. 87

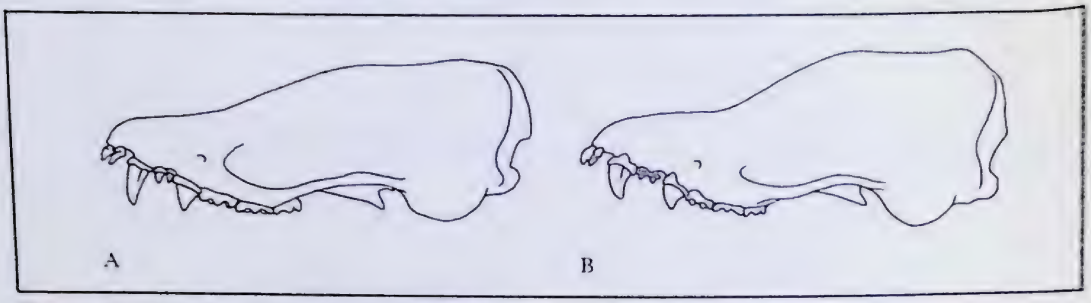


Figure 26. Profile of the skulls of (a) *M. septentrionalis* and (b) *M. keenii*.

18(14) Skull with occiput unusually elevated (Figure 27a) ........................................ *Myotis volans**, p. 83

Skull with occiput not elevated as above (Figure 27b) .......... 19

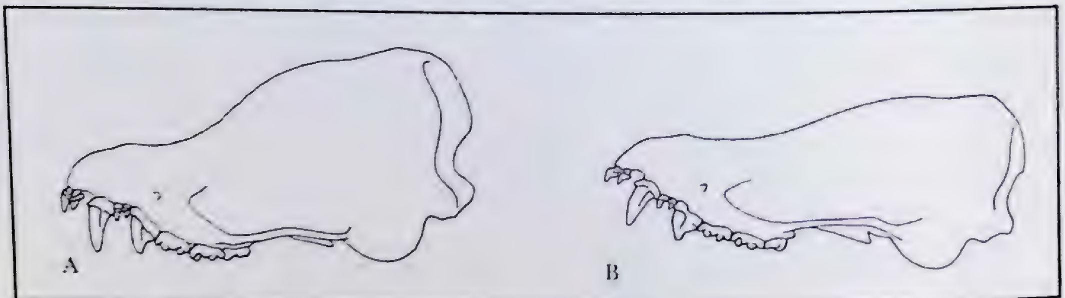


Figure 27. Profile of the skulls of (a) *M. volans* and (b) *M. lucifugus*.

*For critical discrimination of *M. volans* from *M. lucifugus* and *M. yumanensis*, see Appendix, part C.

19(18) Skull with forehead gradually sloping (Figure 28a); covariation of slope index and MW to left of line in Figure 29 . . . . . . . . . . . . . . . . . . . . . *Myotis lucifugus**, p. 68

Skull with forehead steeply sloping (Figure 28b); covariation of slope index and MW to right of line in Figure 29 . . . . . . . . . . . . . . . . . . . . . *Myotis yumanensis*, p. 78

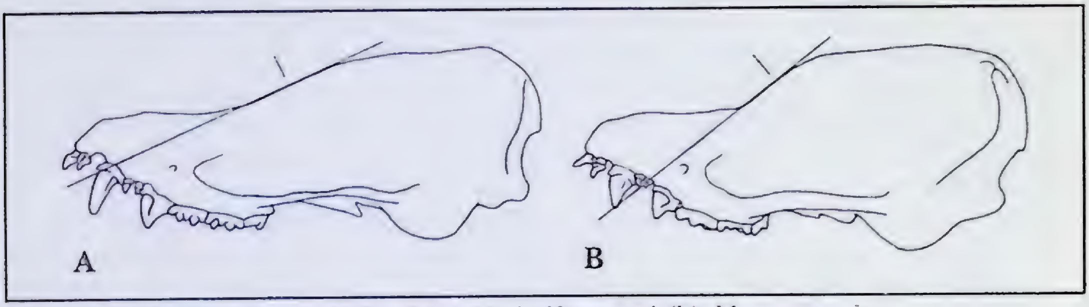


Figure 28. Profiles of the skulls of (a) *M. lucifugus* and (b) *M. yumanensis*.

*The skull of *M. sodalis* resembles that of *M. lucifugus* but has a more distinct sagittal crest.

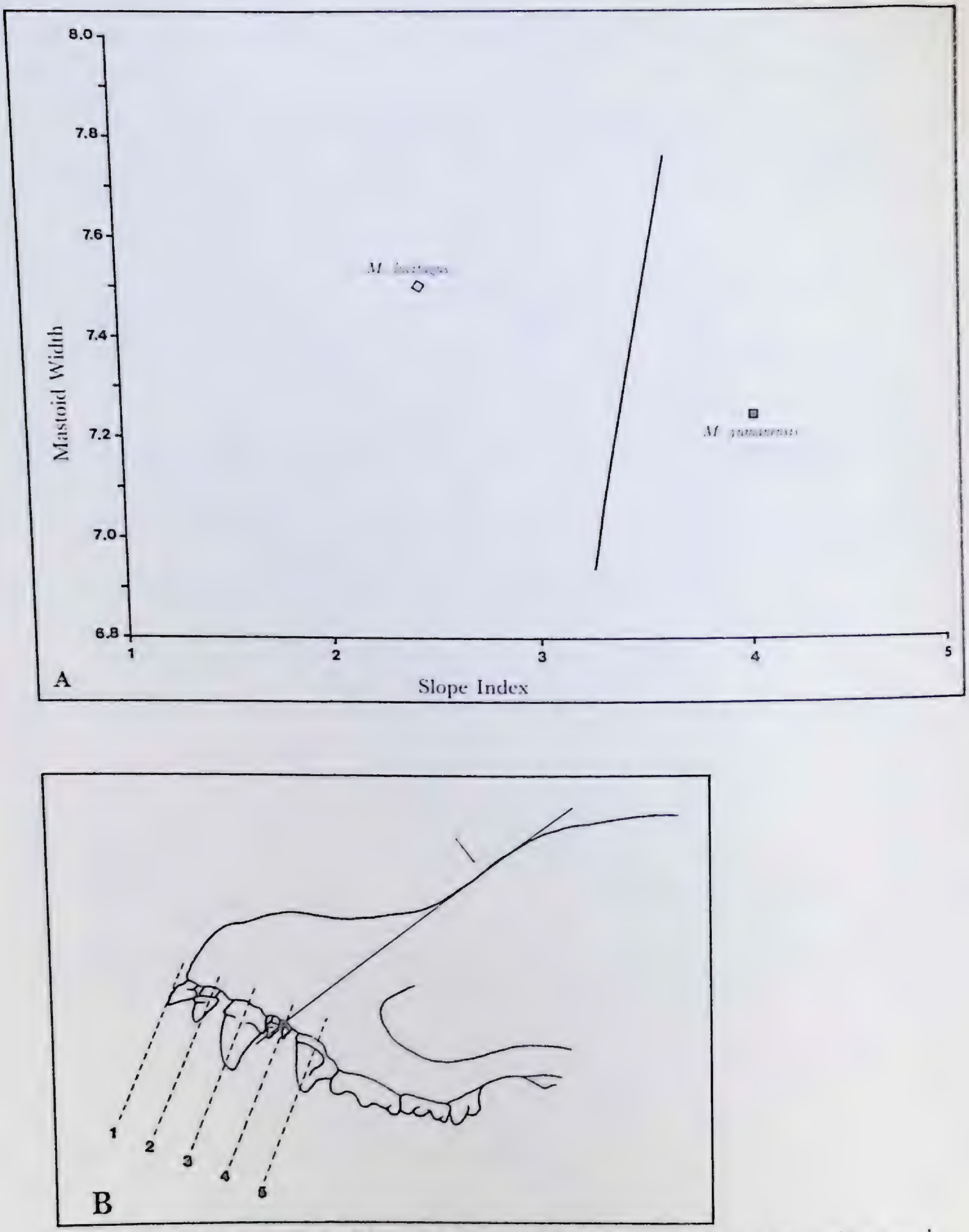


Figure 29. (a) Covariation of frontal slope index and mastoid with in *M. lucifugus* and *M. yumanensis*. (b) Scale used to assign slope index (point at which slope line intersects alveolar line). The slope line is tangential to a point at the location of the cribriform plate (line at right angle to slope line).

## Family VESPERTILIONIDAE Gray, 1821

(f.L *vespertilio* bat; *vesper* evening)

**Plain-nosed bats** | **Vespertilionidés**

The bats of this family are, relative to the size range in the order as a whole, small to medium-sized (FA 24–90), possess plain, unadorned muzzles, relatively small eyes and moderately long to large ears with a well-developed tragus. Sexual dimorphism is not pronounced, with females usually averaging slightly larger than males [4, 6]. The ears cannot be moved as a whole as we know it in other mammals, but the outer edge can be shortened folding the ear and curving it backwards. In resting or hibernating *Euderma* and *Plecotus* the long ears can be curled back this way, so that only the tragi stick up. The number of folds in the ear corresponds to the number of transverse cartilaginous ridges in the outer ear, which varies with the size of the ear, being larger in long-eared species. The tail is long and incorporated in the interfemoral membrane. The pelage is composed of overhair and underhair. Overhair is distinguished by an expanded distal portion comprising ⅓ to ½ of the length of the hair. A distinct medulla is absent. The microscopic structure of the hair, in particular of the cuticular scales, is usually distinct in different genera (Figure 30). Pararhinal glands are present, and often well developed (*Plecotus*, *Euderma*, *Pipistrellus*, *Eptesicus*). There are usually two pectoral mammae, sometimes four (*Lasiurus*). The skull has the premaxillae and upper incisors widely separated. There are 28–38 teeth. Three upper and lower molars on each side are always present, which have a pronounced W-shaped ectoloph. The ulna is much reduced and proximally fused with the radius. The second digit has a well-developed metacarpal and one phalanx, the third, fourth and fifth digits have three phalanges each. The legs are long; the fibula is thin and its proximal end often cartilaginous. All species can walk well, with the anterior part of the body being supported by the distal end of the forearm (thumb pads).

Most bats in this family are insectivorous, a few partially piscivorous, and one exclusively so. The Vespertilionidae are the most widely distributed family of bats, occurring on all continents, except Antarctica, and all major tropical and temperate islands.

The family is subdivided in 6 subfamilies, 36 genera and comprises approximately 315 species. The subfamilial and suprageneric classification of the family is still unstable. Most Canadian vespertilionids belong to the subfamily Vespertilioninae. *Antrozous*, the only possible exception, was customarily placed in the subfamily Nyctophilinae, but this appears now to be incorrect (see comments under *Antrozous*). The relationships within the Vespertilionidae, suggested by the results of studies of chromosomal banding, are at variance with current subfamilial and suprageneric classification. For example *Eptesicus* and *Pipistrellus* are usually placed in the same tribe [2, 5], however recent chromosomal banding data suggest that *Pipistrellus* is closer to *Myotis* [1]. The phylogenetic division of the taxa studied thus far, based on banding patterns, includes a *Myotis*-like group with *Myotis*, *Pipistrellus*, *Lasiurus*, *Plecotus*, *Idionycteris* and *Lasionycteris* and an *Eptesicus*-like group with *Eptesicus*, *Rhogeesa*, *Nycticeius* and *Antrozous*.

## References

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[4] Myers, P., 1978
[5] Tate, G.H.H., 1942
[6] Williams, D.F., and J.S. Findley, 1979

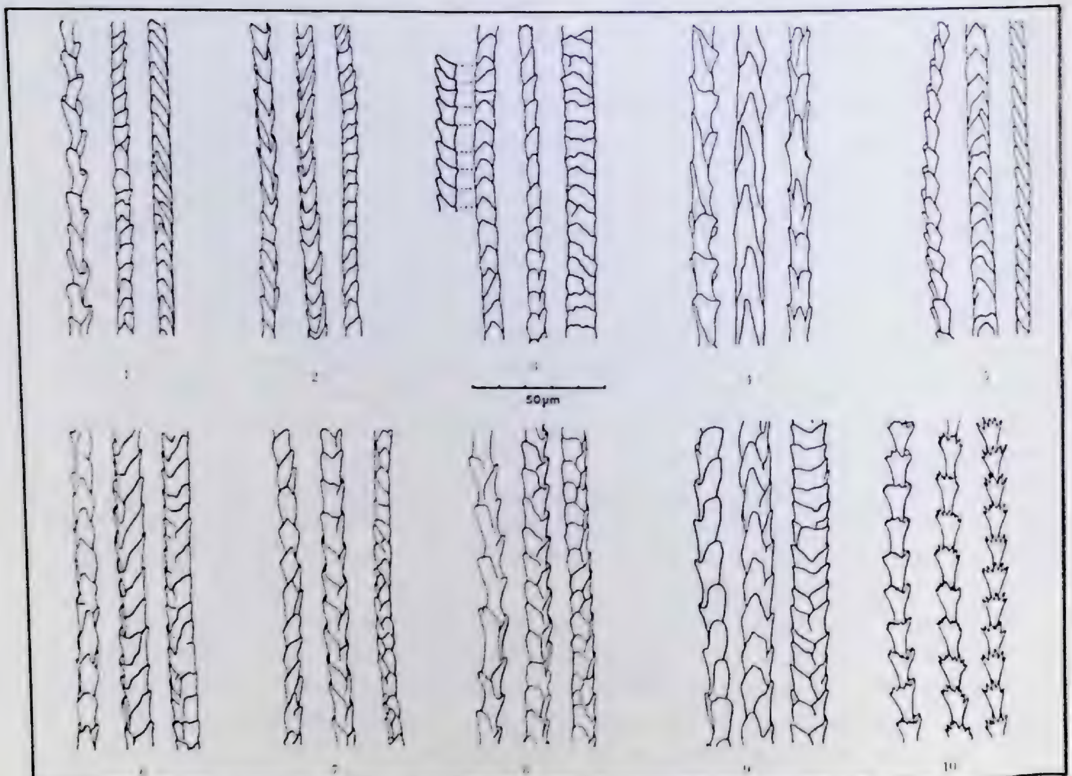


Figure 30. Cuticular scale patterns in Canadian bats showing proximal, median and distal sections. 1) *Myotis lucifugus*; 2) *Pipistrellus subflavus*; 3) *Lasionycteris noctivagans*; 4) *Lasiurus borealis*; 5) *Plecotus townsendii*; 6) *Euderma maculatum*; 7) *Eptesicus fuscus*; 8) *Nycticeius humeralis*; 9) *Antrozous pallidus*; 10) *Tadarida brasiliensis*. The outline drawings are based on scanning electron micrographs taken by the National Research Council.

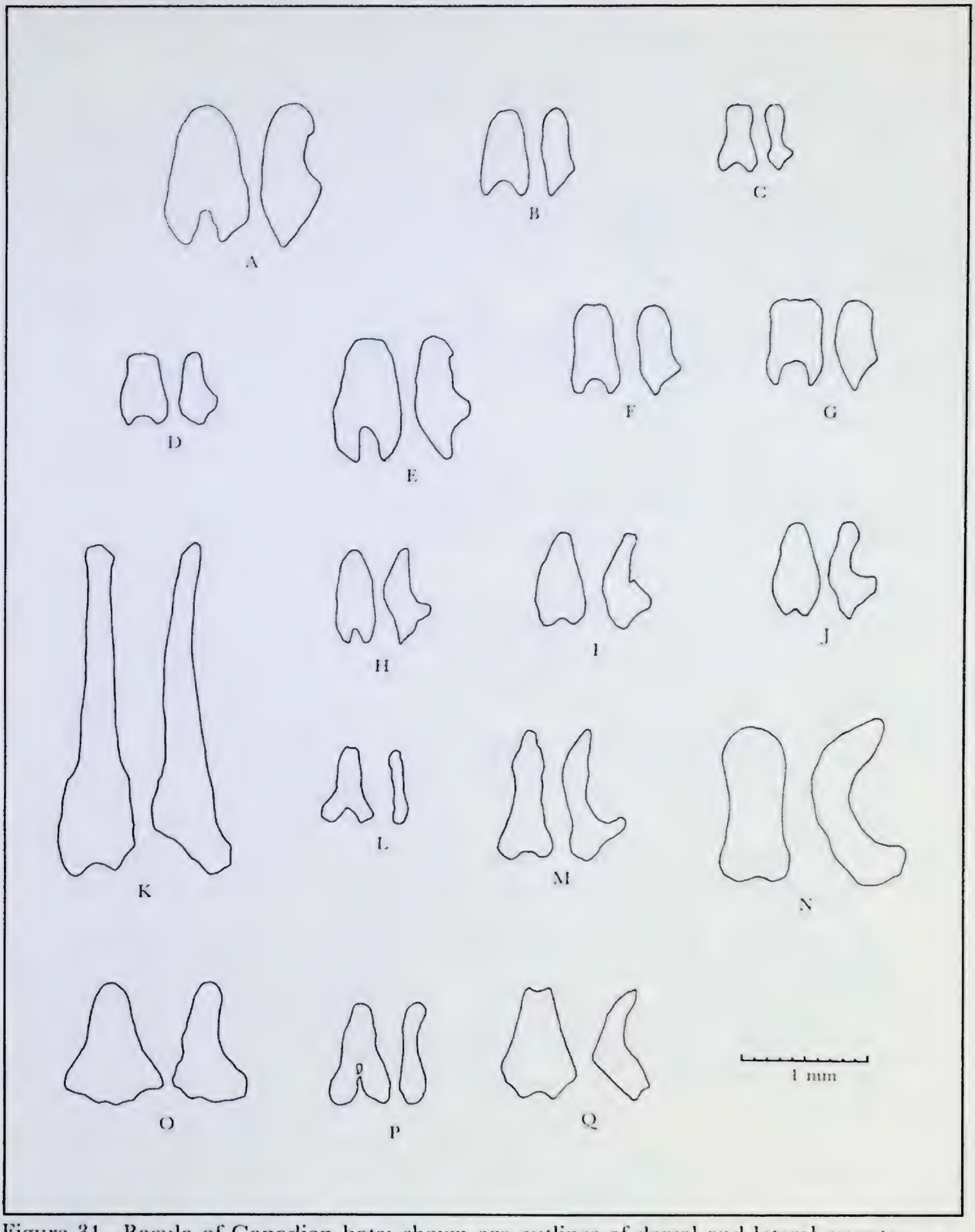


Figure 31. Bacula of Canadian bats; shown are outlines of dorsal and lateral aspects with the proximal end pointing down and the ventral side to the left (lateral aspect). The means and standard deviations for length, width and height and sample size are listed in Table 4. a) *Myotis lucifugus*; b) *Myotis yumanensis*; c) *Myotis volans*; d) *Myotis keenii*; e) *Myotis septentrionalis*; f) *Myotis evotis*; g) *Myotis thysanodes*; h) *Myotis californicus*; i) *Myotis ciliolabrum*; j) *Myotis leibii*; k) *Lasionycteris noctivagans*; l) *Pipistrellus subflavus*; m) *Lasiurus borealis*; n) *Lasiurus cinereus*; o) *Plecotus townsendii*; p) *Eptesicus fuscus*; q) *Antrozous pallidus*.

Table 4: Means (X), standard deviations (SD) and observed range (OR) of three bacular measurements of adult specimens of 16 species of Canadian bats

| | | Length of baculum | | | Width of baculum | | | Height of baculum | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | X̄ | SD | OR | X | SD | OR | X | SD | OR |
| *M. lucifugus* | 22 | 1.057 | 0.1738 | 0.60–1.33 | 0.604 | 0.0846 | 0.49–0.79 | 0.518 | 0.0726 | 0.42–0.63 |
| *M. yumanensis* | 4 | 0.630 | 0.0716 | 0.57–0.71 | 0.330 | 0.0478 | 0.28–0.38 | 0.265 | 0.0129 | 0.25–0.28 |
| *M. volans* | 4 | 0.535 | 0.0858 | 0.41–0.60 | 0.316 | 0.0568 | 0.24–0.36 | 0.212 | 0.0359 | 0.16–0.24 |
| *M. keenii* | 1 | 0.58 | | | 0.36 | | | 0.28 | | |
| *M. septentrionalis* | 7 | 0.950 | 0.0978 | 0.80–1.60 | 0.484 | 0.0478 | 0.42–0.55 | 0.353 | 0.0415 | 0.29–0.41 |
| *M. evotis* | 7 | 0.719 | 0.0758 | 0.64–0.83 | 0.400 | 0.0351 | 0.36–0.45 | 0.307 | 0.0509 | 0.25–0.37 |
| *M. thysanodes* | 2 | 0.676 | 0.0481 | 0.64–0.71 | 0.455 | 0.0071 | 0.45–0.46 | 0.315 | 0.0212 | 0.30–0.33 |
| *M. californicus* | 6 | 0.723 | 0.0631 | 0.62–0.79 | 0.353 | 0.0378 | 0.31–0.41 | 0.322 | 0.0426 | 0.27–0.38 |
| *M. ciliolabrum* | 17 | 0.769 | 0.0800 | 0.64–0.92 | 0.358 | 0.0452 | 0.26–0.42 | 0.349 | 0.0519 | 0.25–0.47 |
| *M. leibii* | 5 | 0.800 | 0.0696 | 0.72–0.89 | 0.350 | 0.0469 | 0.30–0.40 | 0.340 | 0.0548 | 0.26–0.40 |
| *P. subflavus* | 4 | 0.592 | 0.0171 | 0.57–0.60 | 0.400 | 0.0183 | 0.38–0.42 | 0.130 | 0.0082 | 0.12–0.14 |
| *L. noctivagans* | 2 | 2.720 | 0.0283 | 2.70–2.74 | 0.625 | 0.0212 | 0.61–0.64 | 0.595 | 0.0212 | 0.58–0.61 |
| *L. borealis* | 5 | 0.976 | 0.0921 | 0.82–1.07 | 0.470 | 0.0200 | 0.44–0.49 | 0.560 | 0.0381 | 0.44–0.61 |
| *L. cinereus* | 2 | 1.345 | 0.0354 | 1.32–1.37 | 0.480 | 0.1131 | 0.40–0.56 | 0.810 | 0.0707 | 0.76–0.86 |
| *P. townsendii* | 2 | 0.945 | 0.0636 | 0.90–0.99 | 0.640 | 0.1838 | 0.51–0.77 | 0.450 | 0.2121 | 0.30–0.60 |
| *E. fuscus* | 17 | 0.884 | 0.0881 | 0.70–1.02 | 0.525 | 0.0675 | 0.41–0.63 | 0.224 | 0.0429 | 0.16–0.33 |

## Genus *Myotis* Kaup, 1829

(f. Gk *mus* mouse; *ous* genit. *ōtos* ear)

*Myotis* is a rather primitive genus, lacking any unusual specializations. The snout is simple, the ears slightly curved or straight and separate, a well-developed tragus, at least one-half as high as the ear, is present. The number of teeth is large (38). The dental formula is as follows: i2/3; c1/1; p3/3; m3/3. In some species of this genus P2 is absent. The smallest and largest species in the genus range in size from those with a forearm length of slightly less than 30 mm and a body weight of about 5 g to those with a forearm length of 68 mm and a weight of 45 g.

*Myotis* is the most cosmopolitan genus of bats, being found on all continents, except Antarctica, and large islands and at higher latitudes to the limits of tree growth. The genus has its greatest diversity in warm temperate regions. The majority of species of the Palearctic and Nearctic bat faunas belong to the genus.

Approximately 90 species are recognized in the world, and may be divided in three phenetic groups, corresponding to the subgenera *Myotis*, *Selysius* and *Leuconoe* [2]. The subgenus *Myotis* comprises species characterized by long ears, narrow braincases, relatively long tapering rostra, reduced accessory molar cusps, and teeth that are more highly sectorial. Flight in this group is slow, but highly manoeuvrable. Food can be gleaned from foliage and other surfaces. *Selysius* is characterized by small feet; increased plagio-patagial breadth; through lower attachment of the wing membrane on the foot; the presence of a well-developed keel; adaptations on the ventral surface of the uropatagium, which facilitate the aerial capture of insects; short jaws; and small size. *Leuconoe* is characterized by larger size, large feet, short tail, short tibia, short wings, longer dentary, less reduced lower premolars, less tapered rostrum, and teeth that are less sectorial. Flight is rapid and direct and there is presumably more specialized use of the feet in feeding and a reduced use of the uropatagium as an insect net.

The characters that define the subgenera are often not clearcut and are not always present in the combinations outlined. If all species of the genus are considered, we find some species that combine characters of different groups. This overlap in subgeneric characters casts doubt on the subgeneric classification of the genus. Recent electrophoretic data conflict with the current subgeneric arrangement [3] and point to the need for further work.

The species occurring in Canada can, however, be arranged on the basis of the above phenetic group as follows:

Subgenus *Myotis* with *M. evotis*, *M. keenii*, *M. septentrionalis*, *M. thysanodes*
Subgenus *Selysius* with *M. californicus*, *M. ciliolabrum*, *M. leibii*
Subgenus *Leuconoe* with *M. lucifugus*, *M. yumanensis*, *M. volans*

The karyotypes of North American species of the genus that have been studied are uniform, 2N = 44; FN 50 [1].

### References


[1] Baker, R.J., and J.L. Patton, 1967
[2] Findley, J.S., 1972
[3] Herd, R.M., 1983
[4] Miller, G.S., Jr., and G.M. Allen, 1928

## *Myotis lucifugus* (Le Conte)
(f. L *lux* genit. *lucis* light; *fugere* to flee)

**Little Brown Bat** — **Vespertilion brun**

1831 *Vespertilio lucifugus* Le Conte, *in* McMurtries's Animal Kingdom . . ., vol. 1, p. 431
1871 *Myotis lucifugus* Miller, N. Am. Fauna 13:59
Type locality: Georgia; probably the Le Conte plantation, near Riceboro, Liberty County.

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 309 | 307 | 275 | 90 | 27 | 35 |
| **$\bar{X}$** | 87.2 | 37.4 | 10.0 | 37.0 | 13.8 | 7.9 |
| **SD** | 4.67 | 4.23 | 0.95 | 1.35 | 0.81 | 1.58 |
| **CV** | 6.45 | 11.35 | 9.56 | 3.66 | 5.91 | 20.03 |
| **OR** | 60–102 | 25–55 | 8–12 | 34–40 | 12.5–15.5 | 5.5–11.0 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 130 | 130 | 130 | 130 | 130 | 130 |
| **$\bar{X}$** | 14.4 | 7.7 | 4.0 | 5.1 | 5.3 | 5.6 |
| **SD** | 0.42 | 0.21 | 0.15 | 0.17 | 0.16 | 0.19 |
| **CV** | 2.97 | 2.75 | 3.79 | 3.41 | 3.13 | 3.48 |
| **OR** | 13.4–15.7 | 7.21–8.21 | 3.5–4.4 | 4.6–5.5 | 4.8–5.8 | 4.6–6.3 |

### Description (Colour Plate I)

A small to medium-sized species among Canadian bats, wingspan 22–27 cm. Colour of fur variable, upperparts yellowish or olive brown to dark brown or nearly black; underparts conspicuously lighter in colour; juveniles generally darker than adults; in adults long hairs on back with glossy tips giving pelage a characteristic metallic sheen; base of hairs dark. Fur relatively long, longer hairs on back usually 9–10 mm long; ventral surface of wing with thin fur extending approximately from knee to a point three-quarters down humerus, dorsal surface of interfemoral membrane also thinly furred down to the knees; a few inconspicuous hairs scattered along free edge of uropatagium. Flight membranes and ears dark brown.

Ears moderately long, pressed forward their tips reaching to nostril; anterior edge convex, tips bluntly rounded; tragus blunt and about half as long as ear, its inner margin nearly straight, outer margin only slightly convex, with a small rounded basal lobe.

Foot large, exceeding half length of tibia (ratio foot/tibia 0.53–0.56); terminal joints of toes with a few stiff hairs extending to tip of claw or beyond. Calcar, not keeled, exceeding free border of uropatagium in length. Metacarpals showing gradation of diminishing lengths from third to fifth metacarpal.

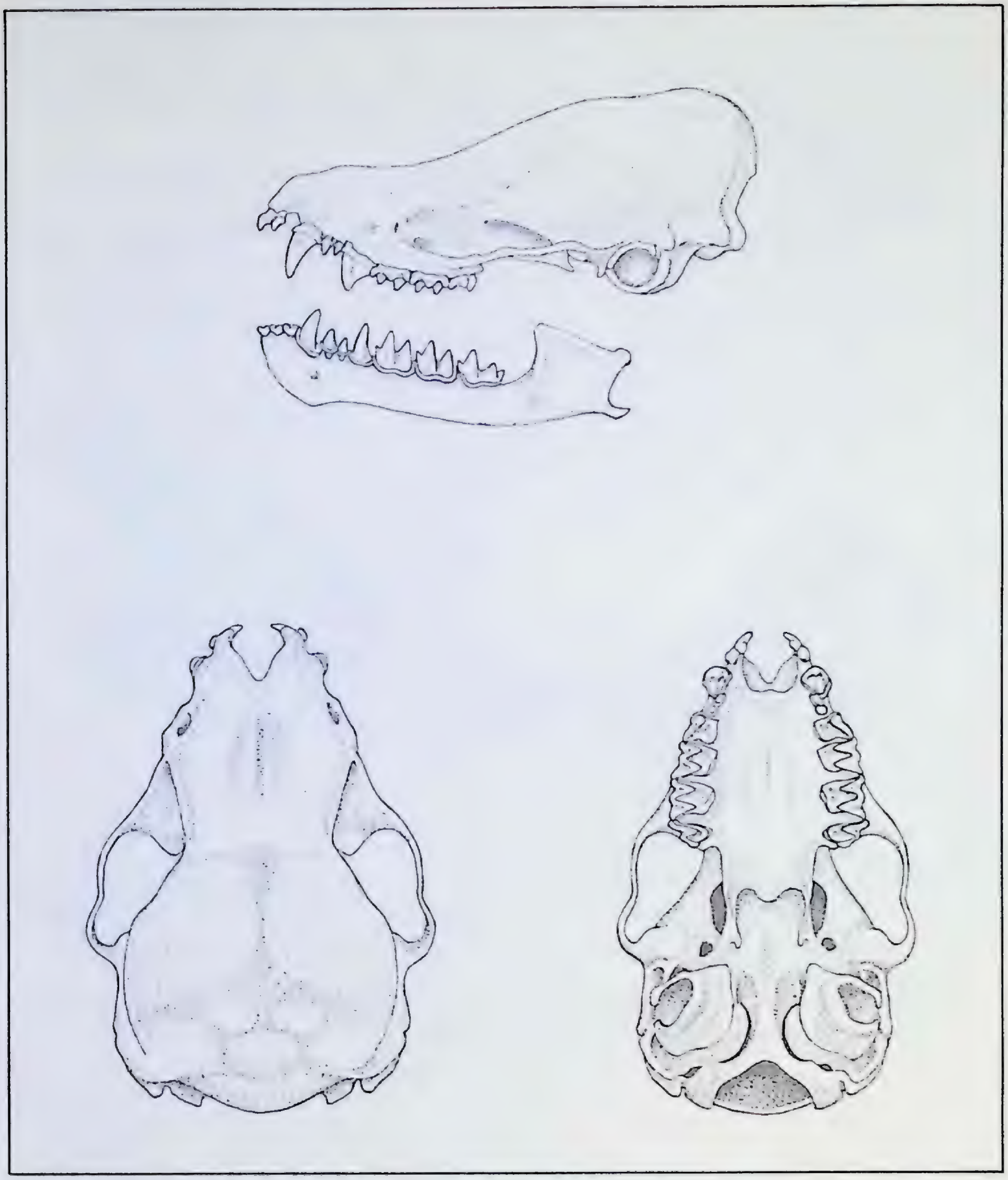

Figure 32. Skull of *Myotis lucifugus*

Skull with relatively short rostrum and gradually sloping forehead. Teeth typical of genus; length of maxillary toothrow generally less than width across molars (M3–M3). Baculum saddle-shaped with distal extremity knob-like, flaring out posteriorly, and ventral side deeply concave; about 1 mm long (Figure 31, Table 4).

Similar Species: *Myotis yumanensis*: dull, shorter fur, paler ears and skull with more steeply sloping forehead, smaller; usually FA<37; SL<14; MW<7.3. In areas of sympatry in southern British Columbia specimens of *M. yumanensis* and *M. lucifugus* are sometimes difficult to identify [32]. *M. volans*: small keel on calcar, venter nearly the same colour as dorsum; foot/tibia ratio<0.50 and relatively dense fur on ventral surface of plagiopatagium to a line between elbow and knee. *M. keenii* and *M. septentrionalis*: longer ears, reaching beyond the nostrils when bent forward and a long, narrow, pointed tragus, length of maxillary toothrow exceeding M3–M3 width. *M. sodalis*: keeled calcar and hairs on toes not extending beyond tips of claws. *M. leibii* and *M. californicus*: smaller (FA 30–35); smaller feet (HF 5–8) and keeled calcar.

### Distribution

The little brown bat is the most common and widely distributed of Canadian bats. It is found from the Atlantic to the Pacific coast and occurs to the limits of the boreal forest. Peripheral localities: *British Columbia*: (1) Lower Post; (2) Victoria; (3) Port Hardy; (4) Kent Inlet; (5) Hotspring Island; (6) Masset. *Manitoba*: (7) Herb Lake. *New Brunswick*: (8) Youghall (Bathurst). *Newfoundland*: (9) Makkovik; (10) Burnt Pond N of Badger; (11) Salmonier; (12) Codroy; (13) South Brook, near Corner Brook. *Nova Scotia*: (14) Cape North; (15) Port Joli. *Northwest Territories*: (16) Hay River. *Ontario*: (17) Favourable Lake; (18) Moose Factory; (19) Geikie Island. *Prince Edward Island*: (20) Mount Herbert. *Quebec*: (21) Knob Lake, 11 km NW of Schefferville; (22) MacDonald Lake, 96 km E of Port-Menier; (23) Rupert-House. *Saskatchewan*: (24) Uranium City. *Yukon*: (25) Stewart River; (26) Mayo; (27) Haines Junction.

In the United States it is found in southern Alaska and the greater part of the lower 48 states, and south to the central highlands of Mexico.

Distribution of *Myotis lucifugus*

## Systematics

*Myotis lucifugus* is a variable species with respect to size and colour, on the basis of which six subspecies are currently recognized. Four of these occur in Canada. Geographic variation in this species needs to be analyzed and the subspecies re-evaluated.

*M. l. alascensis* Miller, 1897, N. Am. Fauna 31:63.
A dark-coloured form similar in size to *M.l. lucifugus*, ears, nose and membranes very dark, approaching black. Distribution: the west coast of North America from southeastern Alaska to California, in Canada most of British Columbia.

*M. l. carissima* Thomas, 1904, Ann. and Mag. Nat. Hist., ser. 7, vol. 13:383.
This form differs from the others in its paler colour. Distribution: semi-arid parts of the western United States; in Canada, the dry interior of southern British Columbia (Okanagan Valley and vicinity of Kamloops) and southern Alberta [48].

*M. l. lucifugus* (Le Conte), 1831.
Colour brown, paler than *alascensis* and *pernox*, darker than *carissima*. Distribution: eastern and midwestern United States; in Canada, from the Atlantic provinces to Alberta.

*M. l. pernox* Hollister, 1911, Smithson. Misc. Collect. 56(26):4.
Larger and with darker flight membranes than *lucifugus*. The validity of this subspecies is doubted by some. Distribution: northwestern Canada (Alberta, northern British Columbia and the Yukon) and interior Alaska [56].

*M. lucifugus* is closely related to the Mexican *M. fortidens* and *M. yumanensis* of western North America. *M. lucifugus* and *M. yumanensis* were suspected to hybridize occasionally in areas of sympatry [30, 42], based on the occurrence of individuals morphologically intermediate between the two. However, a recent electrophoretic study of proteins of *M. lucifugus* and *M. yumanensis* from the Okanagan Valley, by Herd [31, 32], does not support this hypothesis.

## Biology

The little brown bat lives nearly anywhere that some trees and water are found. It prefers to hunt low over water, although it also forages among trees at heights between 3–6 m and over lawns and streets in built-up areas. It roosts in natural cavities, under loose bark and in crevices, as well as in buildings, where it may be found in attics, behind shutters or siding, or under shingles. Maternity colonies are now most commonly found in buildings and less in suitable natural sites. Microclimatic requirements such as optimal temperature conditions that favour the growth of the young are apparently important in the selection of sites [16]. The availability of suitable maternity sites may be a limiting factor to the distribution and abundance of the species. Habitat

The food of the little brown bat includes a variety of insects varying in size from 3–10 mm long [2], including Diptera, Ephemeroptera, Trichoptera, Lepidoptera, Isoptera, Homoptera and Coleoptera [6, 11, 24, 52, 53]. Aquatic insects such as midges (Chironomids), mayflies and caddis flies predominate. A very efficient hunter, this bat may fill its stomach in less than 15 minutes. Food passes through the digestive system rapidly. In an active bat it takes only between 35 and 54 minutes for the first droppings to pass, although it may take several hours for all food to pass [10]. It is probable that the animal fills and empties its digestive tract two or more times during the night. Wild pregnant females were reported to consume an average of 2.5 g of insects nightly, lactating females 3.7 g, and juveniles 1.8 g [2]. Food

*M. lucifugus* itself falls prey to other animals occasionally. Predation by small carnivores, mice, birds of prey and snakes have been reported [24]. None of these are specialized predators of bats, however, and predation may not be a serious mortality factor. Ectoparasites, particularly fleas, mites and, in the roosts, bat bugs are common. The level of infestation varies seasonally as well as between sex and age groups [21]. Predators and Parasites

Populations of *M. lucifugus* in Canada are characterized by a preponderance of males among the adult age class, judging from counts in hibernacula [21]. The sex ratio after birth and during the non-volant stage in the young is 1:1. The survival rate is relatively low during the first winter because the young do not attain full adult weight and are less likely to survive hibernation. Afterwards the survival rate is much higher and apparently remains relatively constant. There is no strong evidence of differential mortality. However, the preponderance of males encountered in the hibernacula may result from a higher mortality among females in higher latitudes, induced by the harsher climatic conditions and stress of pregnancy and lactation [33]. Differences in survival rates (0.799 for males, 0.755 for females [33]) based on data collected in southeastern Ontario, however, are insufficient by themselves to account for the observed sex ratios in hibernacula. Changes in sex ratios of hibernating populations suggest that part of the observed disparity may result from some females spending part of the time hibernating elsewhere or in inaccessible parts of the cave. Population age structure and survival rates are not well known, but reproductive potential is low and longevity is high (the record is in excess of 31 years for a male banded as an adult in southeastern Ontario) [24]. Population

*M. lucifugus* emerges relatively late at dusk and forages most actively in the first two or three hours after sunset. After this initial feeding period the bats usually congregate in night roosts, confined spaces that may function to conserve heat, which keeps them active and digestion progressing at a more rapid rate [24]. The period in the night roost is followed by a second foraging period. The proportion of time spent roosting and feeding varies daily as well as seasonally, depending on the reproductive condition of the animal, abundance of prey and air temperature [3]. Lactating females do not use night roosts but return to the Activity and Behaviour

maternity colony between foraging periods. Greatest use of night roosts occurs in late summer after the young have become volant. Cool temperatures and low abundance of prey result in long roosting periods, a behavioural response thought to conserve energy [3].

Little brown bats appear to detect their prey by echolocation at a range of 1 m or less and are adept at foraging in swarms of insects [25]. Insects are usually captured on the wing or are gleaned off the surface of the water. Observations show that this bat is a capable swimmer if it accidentally falls into the water [43].

The little brown bat produces a high-intensity FM echolocation call [25, 28]. The fundamental frequency of the echolocation call of a cruising little brown bat sweeps from a high of about 78 kHz to a low of about 40 kHz and has a duration of 1–3 ms [25, 28]. When on a collision course with another bat, the animal will "honk" by sweeping the frequency of the echolocation call down to 25 kHz [25].

Aside from echolocation calls, ten different types of vocalizations have been recorded from this bat [4]. The majority of these are a graded series of agonistic calls, whereas only three, the copulation call, isolation call and double note call, are used in important nonagonistic social contexts, namely mating and mother-infant interactions. The copulation call is uttered repeatedly by adult males immediately after the initiation of mating [5]. The call is not given when a male mates with a torpid female and it presumably communicates the sexual rather than aggressive intentions of the male and pacifies the female. The isolation call is given by juvenile bats and is most commonly heard when the females are leaving or entering the roost; it is also produced by young that have fallen from their roosts. The isolation call aids the mother in locating her young. The double-note call of females is also associated with mother-infant interactions. There is experimental evidence that mother and young recognize each other's calls. Although vocalizations play an important role in mother-young interactions, final acceptance or retrieval of young is preceded by olfactory inspection. Young will attempt to suckle any female, but females only nurse their own young.

The role of olfaction in the behaviour of the species is not well known. The sense of smell is well developed [7] and the development of the pararhinal glands during the mating season strongly suggests its scent may serve some communication function [51]. There is also evidence that this species maintains scent posts near maternity colonies, which could provide cues for orientation by young and perhaps adults as well [12]. There are no visual displays other than the baring of teeth in agonistic encounters [4, 51]. The use of vision and the ability to distinguish patterns in dim light have been demonstrated for this bat [8, 38]. Visual orientation is used, in some cases in preference to echolocation and may be the main mode of orientation during long distance migrations.

The little brown bat is a gregarious species with a simple social structure evidenced by the lack of elaborate forms of behaviour and a limited vocal repertoire [51]. The benefits of the gregariousness appear to be related primarily to thermoregulation (clustering) and reproduction.

Maternity colonies begin to form in spring (April) after the bats come out of hibernation. Numbers of adults in the maternity colonies continue to increase until mid-June. The colonies start to break up in August and by September few bats remain. There is a high degree of attachment to maternity sites, which are used year after year.

The number of bats in a maternity roost varies from a dozen to over a thousand. Early in the season there are few or no adult males, but later on in the summer males appear in increasing numbers in the colony. Males generally live apart during the summer and roost singly or in small groups. From mid-July through August these bats frequent the hibernacula in increasing numbers (swarming), first the adult males and nulliparous females and then later also the postpartum females and young of the year [20, 45]. The animals fly in and out of the caves but only a few actually stay to roost. Most individuals appear to engage in swarming activity for only a few nights. Swarming may function in prenuptial behaviour and acquaint the young with the location of hibernation sites [24], and serves to mix bats from different populations [15]. In September and October they return to the hibernacula to hibernate. Little brown bats may move several hundred kilometres to reach the hibernacula from their summer roosts.

Hibernation

Hibernation may begin as early as late September and may last until mid-May, depending on local climatic conditions. Prior to hibernation the animals become quite fat. Adult males gain weight through the summer and females after completion of moult and lactation. Adults enter hibernation before juveniles, who gain weight more slowly, possibly because they lack experience in capturing insects. During the course of hibernation, weight is lost continuously and by spring the animal weighs about one quarter less than it did in the autumn. Arousal from hibernation exacts a high cost in terms of energy. Normally bats arouse spontaneously only infrequently to urinate or move to another site and thus conserve energy. Frequent arousal caused by disturbance will increase weight loss and, if excessive, may result in increased mortality. The locations selected by *M. lucifugus* for hibernation are characterized by above-freezing temperatures (2°C) and high humidity [21].

Reproduction and Ontogeny

Mating begins in late August, peaks in autumn and may continue through winter [24]. The sperm is stored in the uterus. Ovulation and fertilization are delayed until spring after the female arouses from hibernation. After a gestation period of between 50 and 60 days [54], the female gives birth to a single relatively precocial young between early June and mid-July. Twins are rare. The female gives birth in a head-up position catching the young in her cupped tail membrane as it emerges. Breech presentation is the rule.

The pink-coloured young are born apparently naked, although covered with a thin coat of fine silky hair [54]. The eyes and ears are closed, but the eyes open and the pinnae unfold several hours after birth. Twenty deciduous teeth have erupted at birth, and two more will have appeared by the time the first permanent premolar (P3) erupts at approximately three days of age [22]. When the young attain a forearm length of more than 33.5 mm at approximately two weeks of age [36] all deciduous teeth have been lost. The deciduous incisors and the well-developed claws of the hind feet and thumb enable the young to cling to its mother. Juvenile pelage is acquired between four days and two weeks of age.

The young are left behind when the adult females leave to forage during the night, but are attached to their mothers during the day. They begin to fly by 18 days of age and practise flight at night after the adults have left to feed. At three weeks the young have attained adult size (although weighing less), are weaned, have fully erupted permanent dentition, and have mastered flight. Some females may reach sexual maturity at the end of their first summer but there is a tendency for delay in sexual maturity at higher latitudes [46, 47]. In central Alberta the majority of yearling females do not bear young. Males do not become sexually active in their first year of life.

## References


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## *Myotis yumanensis* (H. Allen)
(named after the type locality)

**Yuma Bat** — **Vespertilion de Yuma**

1864 *Vespertilio yumanensis* H. Allen, Monogr. Bats N. Am., Smithson. Misc. Collect. 7 (publ. 165): 58
1897 *Myotis yumanensis* Miller, N. Am. Fauna 13:66
Type locality: Old Fort Yuma, Imperial County, California, near the present town of Yuma, Arizona.

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 70 | 70 | 70 | 23 | 13 | 7 |
| **$\bar{X}$** | 83.0 | 36.1 | 9.6 | 35.3 | 11.5 | 4.9 |
| **SD** | 4.18 | 3.42 | 0.80 | 1.00 | 2.17 | 0.64 |
| **CV** | 5.06 | 9.49 | 8.38 | 2.85 | 18.95 | 13.03 |
| **OR** | 75–91 | 30–47 | 8–12 | 33–37 | 10–16 | 4–5.7 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 50 | 50 | 48 | 38 | 49 | 49 |
| **$\bar{X}$** | 13.5 | 7.2 | 3.8 | 5.0 | 5.0 | 5.4 |
| **SD** | 0.24 | 0.16 | 0.11 | 0.15 | 0.08 | 0.12 |
| **CV** | 1.76 | 2.25 | 2.90 | 3.06 | 1.65 | 2.41 |
| **OR** | 12.8–14.0 | 6.8–7.4 | 3.4–4.1 | 4.6–5.3 | 4.8–5.3 | 5.1–5.8 |

### Description (Colour Plate I)

*M. yumanensis* closely resembles *M. lucifugus*. Size somewhat smaller, and pelage duller, usually without characteristic sheen and shorter than in *M. lucifugus*, longer hairs on dorsum about 5 mm long, blackish, reddish brown or pale brown. Ears paler than in *M. lucifugus*. Skull similar to that of *M. lucifugus* but smaller, usually with steeply sloping forehead. Baculum in dorsal aspect, triangular, distal tip rounded, base enlarged to knob, with ventral groove, approximately 0.6 mm long (Figure 31, Table 4).

Similar Species: *M. lucifugus*: longer, glossy pelage, basal fur on shoulders usually darker; ears and naked parts of face darker; skull with flatter forehead. See comments under *M. lucifugus*. *M. yumanensis* can be distinguished from other small brown bats in its range by the same characters listed in the account of *M. lucifugus*.

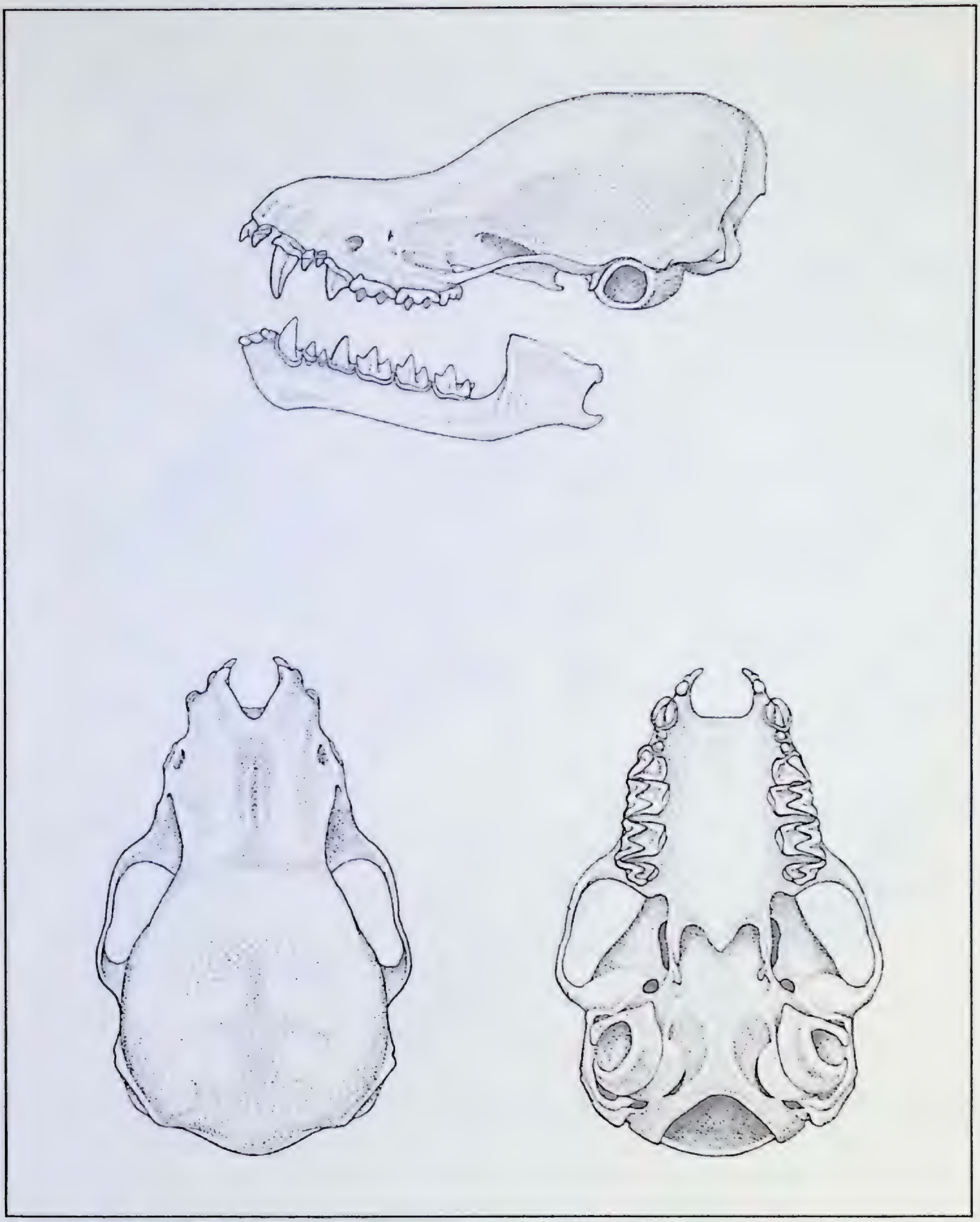

Figure 33. Skull of *Myotis yumanensis*

## Distribution

The Yuma bat occurs in western North America from British Columbia to central Mexico. In Canada, the species is not found east of the Rocky Mountains. Peripheral localities: *British Columbia*: (1) Kamloops; (2) Sicamous; (3) Creston; (4) Mount Lehman; (5) Duncan; (6) Port Hardy; (7) Kimsquit; (8) Alston Cove, Princess Royal Island.


Distribution of *Myotis yumanensis*

## Systematics

*M. yumanensis* is currently divided into seven subspecies, of which only two occur in Canada.

*M. y. saturatus* Miller 1897, N. Am. Fauna 13:68.
A dark-brown to chestnut form with black ears and membranes. Distribution: Coastal area west of the Cascade Range and southwestern British Columbia including Vancouver Island.

*M. y. sociabilis* H.W. Grinnell 1914, Univ. Calif. Publ. Zool. 12:318.
A pale-yellowish or greyish-brown form with pale ears and membranes. Distribution: Southern California and to the north areas east of the Cascade Range; in British Columbia, the arid southern interior.

*M. yumanensis* appears to be closely related to *M. lucifugus*. The two species probably evolved comparatively late in the Pleistocene from a common ancestral population, which split into two isolated populations, one eastern and the other western. The present ranges of the two species partially overlap and in areas of sympatry occasional hybridization has been suspected on the basis of the occurrence of individuals that are morphologically intermediate [4, 6]. However, protein electrophoresis of muscle tissue, plasma and erythrocytes from both species in the Okanagan Valley has shown them to be genetically distinct, thus showing the suspected hybridization there to be unfounded [5].

## Biology

The Yuma bat seems to have an even greater affinity for water than its close relative, the little brown bat [5], and, being found in more open areas, it appears to be less dependent on trees. Its selection of roosting and hibernation sites appears to be similar to that of *M. lucifugus*. This species emerges when it is nearly dark and feeds in similar places as *M. lucifugus*. It rarely flies higher than 10 m above the ground. Observations on the feeding behaviour of *M. yumanensis* and *M. lucifugus* in the Okanagan Valley suggest that they select different places to hunt. *M. yumanensis* preferred to feed low over flowing water, while *M. lucifugus* foraged over bluffs, lakes, and among trees. In the Okanagan Valley, major prey included Trichoptera and Ephemeroptera, and significant differences in the proportions of the kinds of insects eaten by *M. yumanensis* and *M. lucifugus* were found [5]. Elsewhere, this species is known to feed on relatively soft-bodied insects including Diptera, Isoptera, Lepidoptera and Coleoptera [2, 7]. Unfortunately very little is known of the biology of this species in Canada. Parturition begins in early June and probably finishes by the end of that month in the Okanagan [5]. Females give birth for the first time in the summer following their own birth.

Habitat

Food

Reproduction

## References


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## *Myotis volans* (H. Allen)

(f. L *volare* to fly)

**Long-legged Bat** — **Vespertilion à longues pattes**

1866 *Vespertilio volans* H. Allen, Proc. Acad. Nat. Sci. Phila. p. 282
1914 *Myotis volans* Goldman, Proc. Biol. Soc. Wash. 27:102
Type locality: Cape St. Lucas, Baja California, Mexico

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 50 | 50 | 51 | 49 | 43 | 46 |
| $\bar{X}$ | 95.5 | 42.1 | 9.3 | 39.0 | 13.3 | 7.5 |
| **SD** | 4.49 | 3.04 | 0.87 | 1.52 | 1.42 | 1.04 |
| **CV** | 4.71 | 7.25 | 9.41 | 3.91 | 10.74 | 13.83 |
| **OR** | 83–105 | 30–48 | 7–11 | 36–44 | 8–16 | 5.5–10 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 18 | 18 | 17 | 18 | 17 | 17 |
| $\bar{X}$ | 13.8 | 7.8 | 4.0 | 5.5 | 5.3 | 5.8 |
| **SD** | 0.27 | 0.22 | 0.11 | 0.15 | 0.08 | 0.19 |
| **CV** | 1.99 | 2.82 | 2.85 | 2.81 | 1.52 | 3.31 |
| **OR** | 13.1–14.2 | 7.5–8.2 | 3.8–4.15 | 5.3–5.75 | 5.0–5.4 | 5.5–6.2 |

### Description (Colour Plate I)

A medium-sized bat, wingspan 25-27 cm. Colour of fur varying from reddish-brown to nearly black, ventral side relatively dark, less contrasting than in *M. lucifugus*, ventral surface of wing membrane usually rather densely furred to a line from elbow to knee, free border of the uropatagium bare. Ear and flight membranes blackish brown.

Ears relatively short, with broadly rounded tips, just reaching nostrils when laid forward. Tragus short with small rounded basal lobe. Foot relatively small, length less than half that of tibia (foot/tibia approximately 0.41). Calcar, approximately equal in length to free edge of uropatagium, bearing a distinct keel. Third metacarpal longer than fourth and fifth.

Skull with short rostrum and steeply elevated forehead, occiput high and somewhat inflated; teeth similar to those of *M. lucifugus*, with width across molars (M3–M3) exceeding length of maxillary tooth row. Baculum resembles that of other *Myotis* species in being saddle-shaped but is smaller (Figure 31, Table 4).

Similar Species: *M. lucifugus* and *M. yumanensis* have no keel on calcar and a foot/tibia ratio of 0.50 or more, fur on ventral surface of wing much thinner and less extensive, ventrum contrastingly lighter than dorsum, and ears longer with less rounded tips.

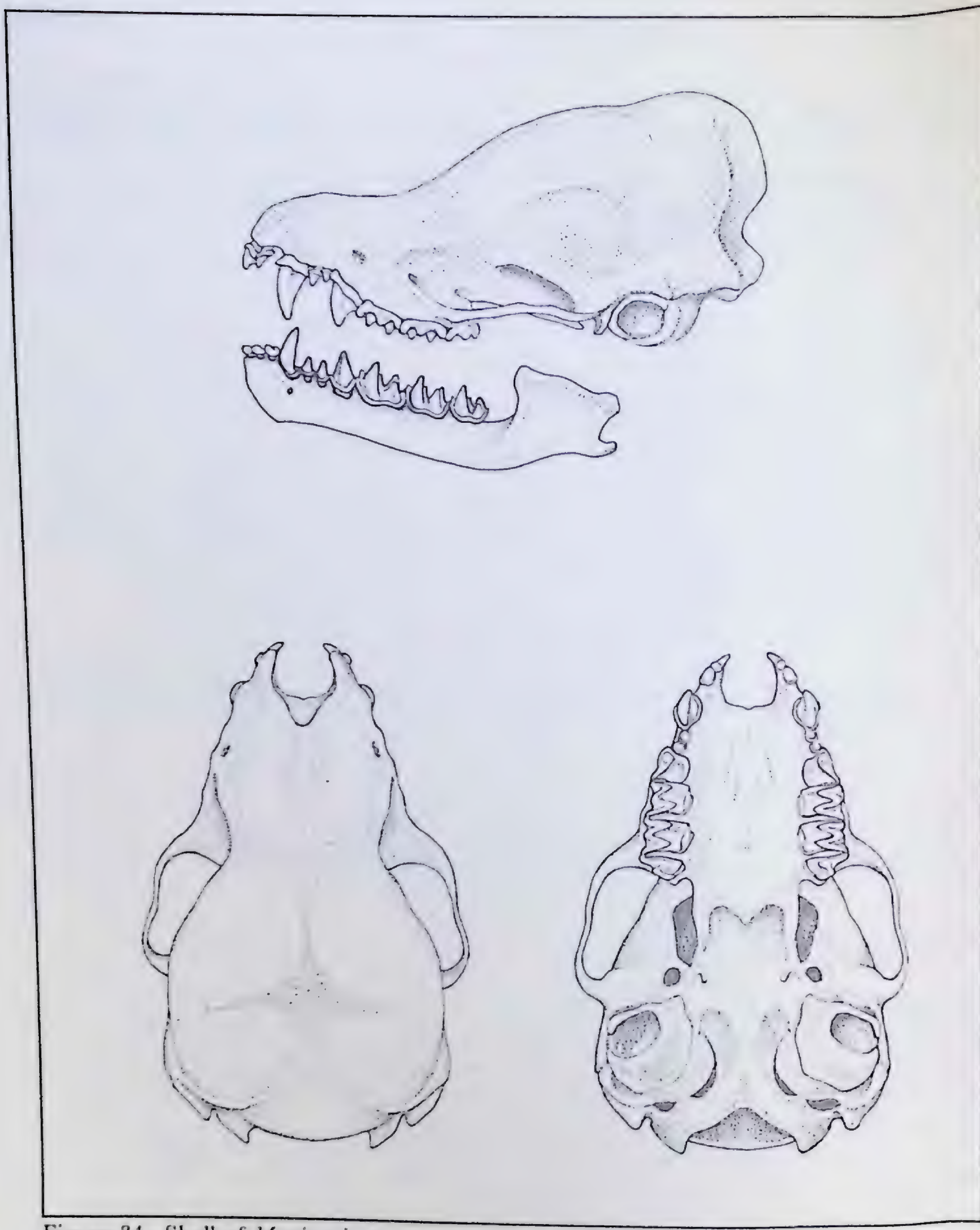

Figure 34. Skull of *Myotis volans*

## Distribution

In Canada the long-legged bat is found chiefly in the mountainous west. Peripheral localities: *Alberta*: (1) Cadomin Cave, near Cadomin; (2) SW of Lethbridge; (3) Writing-on-Stone Provincial Park; (4) Spirit River. *British Columbia*: (5) Atlin; (6) Hazelton; (7) Vancouver; (8) Port Hardy.

In the rest of North America, this bat is distributed throughout the western United States east to the westernmost portions of the Dakotas and Nebraska, Colorado, western Texas and south to central Mexico.


Distribution of *Myotis volans*

## Systematics

Of the four subspecies that have been described, only one is found in Canada: *M.v. longicrus* (True), 1886, Science 8:588.

Bogan [2] has pointed out that the nominate form, which occurs allopatrically in Baja California, is markedly different from the other subspecies in morphology as well as in ecology. The mainland subspecies differ little from one another. All inhabit montane habitats and are rarely found in the arid lowland areas, whereas *M. v. volans* is found at low altitudes in the desert areas and is unknown from montane habitat.

## Biology

Habitat

Little is known of the biology of the long-legged bat. It inhabits forested mountain regions, where it roosts in trees, rock crevices, cracks and crevices in stream banks and in buildings. Maternity colonies have been found in similar places and are probably most often situated in trees. It hibernates in caves. Observations in Alberta suggest that *M. volans* may be more cold tolerant than *M. lucifugus* [5].

Food

The long-legged bat feeds mainly on small moths (96%) and, to a lesser extent, on beetles [1, 7].

Population

Little is known of the population structure and dynamics for this bat. As in *M. lucifugus*, males outnumber females at hibernation sites. A longevity of 21 years has been recorded [6].

Activity and Behaviour

*M. volans* emerges early in the evening when it is still twilight. It flies rapidly and directly and forages high in the open air, usually at treetop level. Later in the evening it hunts closer to the ground and occasionally under the canopy. This aerial hunter catches insects on the wing and does not glean. Its echolocation call consists of a shallow FM sweep (Figure 9), and this bat is capable of detecting prey at a distance of 5–10 m [3].

Reproduction and Ontogeny

This species is moderately gregarious in maternity colonies and during swarming in late summer and hibernation. One young is produced, probably in July. Most juvenile male *M. volans* appear to be sexually active, unlike those of *M. lucifugus* [5].

## References

[1] Black, H.L., 1974
[2] Bogan, M.A., 1978
[3] Fenton, M.B., and G.P. Bell, 1979
[4] Quay, W.B., 1948
[5] Schowalter, D.B., 1980
[6] Tuttle, M.D., and D. Stevenson, 1982
[7] Whitaker, J.O., Jr., C. Maser, and L.E. Keller, 1977

## *Myotis keenii* (Merriam)
(Named after J.H. Keen)

**Keen Long-eared Bat** | **Vespertilion de Keen**

1895 *Vespertilio subulatus keenii* Merriam, Am. Nat. 29:860
1897 *Myotis subulatus keenii* Miller, N. Am. Fauna 13:77
1928 *Myotis keenii keenii* Miller and Allen, Smithson. Inst., U.S. Nat. Mus. Bull. 144, p. 104
Type locality: Masset, Graham Island, Queen Charlotte Islands, British Columbia

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 24 | 24 | 24 | 22 | 19 | 14 |
| **X̄** | 84.8 | 40.0 | 9.1 | 36.0 | 18.5 | 5.2 |
| **SD** | 6.15 | 2.40 | 0.58 | 0.80 | 0.61 | 0.43 |
| **CV** | 7.26 | 6.02 | 6.42 | 2.22 | 3.31 | 8.23 |
| **OR** | 63–93 | 35–44 | 8–10 | 35–38 | 18–20 | 4.3–5.6 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 22 | 21 | 5 | 5 | 22 | 22 |
| **X̄** | 14.6 | 7.4 | 3.8 | 5.0 | 5.6 | 5.5 |
| **SD** | 0.23 | 0.11 | 0.06 | 0.07 | 0.11 | 0.09 |
| **CV** | 1.60 | 1.62 | 1.74 | 1.45 | 1.95 | 1.80 |
| **OR** | 14.2–15 | 7.2–7.6 | 3.7–3.9 | 4.9–5.1 | 5.5–5.9 | 5.3–5.6 |

### Description (Colour Plate II)

A small to medium-sized bat, wingspan 21–26 cm. Fur glossy brown, dark brown on back, lighter, buffy below, dark shoulder spots present; free border of uropatagium with minute, scattered hairs. Ears and flight membranes dark but not black. Ears long, extending beyond tip of nose when laid forward. Tragus long, slender and pointed. Foot relatively large, usually more than half as long as tibia. Calcar long, about half as long as distance from foot to tip of tail, with slight keel. Third, fourth and fifth metacarpals approximately equal in length.

Skull usually with relatively steep sloping forehead; maxillary toothrow usually slightly longer than greatest width across molars (M3M3W); rostrum, and mastoid width relatively narrow. Baculum smaller and differing in shape from that of *M. septentrionalis*, more similar to that of *M. evotis* (Figure 31, Table 4).

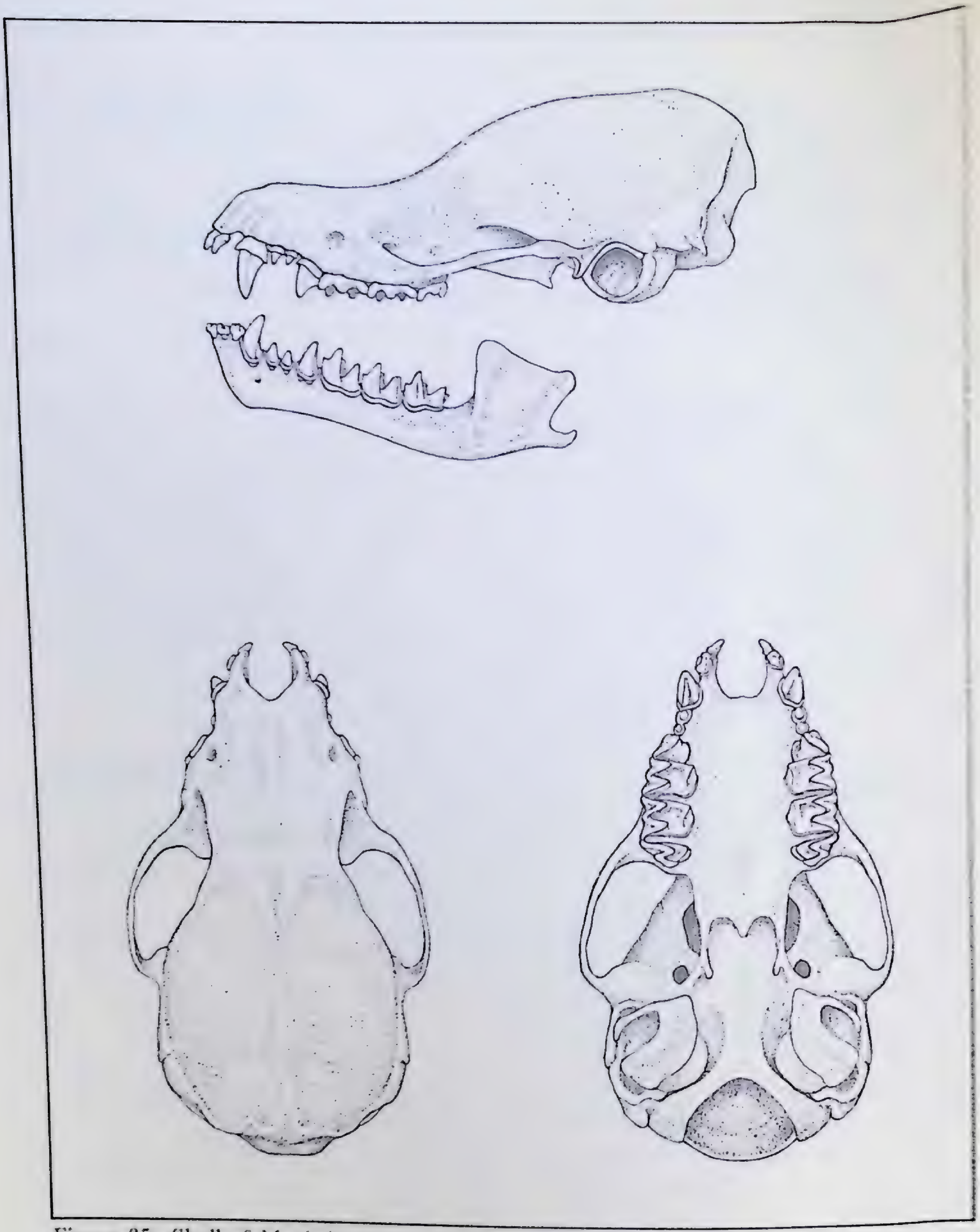

Figure 35. Skull of *Myotis keenii*

Similar Species: *M. evotis*: black ears extending more than 5 mm beyond rhinarium when pressed forward, colour of pelage lighter. *M. septentrionalis*: no dark spot at shoulder; free edge of uropatagium bare; skull with flatter forehead and larger canine. *M. lucifugus*: shorter ears; broader skull with M3–M3 width exceeding length of maxillary toothrow.

## Distribution

*M. keenii* has one of the smallest distributional ranges of any North American bat. The bulk of its range is in British Columbia west of the Coast Mountains extending into southeastern Alaska and northwestern Washington. Peripheral localities: *British Columbia*: (1) Telegraph Creek; (2) Kimsquit; (3) Stuie; (4) NE shore of Cultus Lake; (5) Port Hardy; (6) Rose Harbour; (7) Masset.


Distribution of *Myotis keenii*

## Systematics

*M. keenii* and *M. septentrionalis* were until recently considered to be conspecific, although some authors expressed doubt about the taxonomic status of the two forms [1] or noted differences in their crania [3]. Morphological comparison shows that *M. keenii* and *M. septentrionalis* differ approximately as much from one another as each differs from *M. evotis* [4]. Although the known ranges of *M. keenii* and *M. septentrionalis* do not overlap, and the reproductive isolation of the two forms can at the moment only be inferred on the basis of phenetic differences between them, the available evidence strongly suggests independent specific status for the two forms. Geographic variation in *M. keenii* has not yet been investigated.

## Biology

Very little is known of the biology of *M. keenii*. It appears to be restricted to the dense coastal forest of the Pacific coast. It is thought to be solitary and to roost in tree cavities and rock crevices [2]. It is reported to hunt high along forest edges and over ponds and clearings, flying rather slowly [2].

## References

[1] Barbour, R.W., and W.H. Davis, 1969
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[3] Genoways, H.H., and J.K. Jones, Jr., 1969
[4] van Zyll de Jong, C.G., 1979

## *Myotis septentrionalis* (Trouessart)

(f. L *septentrionalis* northern)

**Northern Long-eared Bat** — **Vespertilion nordique**

1897 *Vespertilio gryphus* var. *septentrionalis* Trouessart, Catal. Mamm. viv. foss., p. 131

1897 *Myotis subulatus* Miller, N. Am. Fauna 13:75

1928 *Myotis keenii septentrionalis* Miller, Smithson. Inst., U.S. Nat. Mus. Bull. 144, p. 105

Type locality: Halifax, Nova Scotia

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 49 | 49 | 47 | 14 | 27 | 21 |
| **X̄** | 86.2 | 37.7 | 9.4 | 36.4 | 16.4 | 7.4 |
| **SD** | 3.29 | 3.38 | 0.90 | 1.42 | 1.17 | 1.50 |
| **CV** | 3.82 | 8.99 | 9.64 | 3.89 | 7.11 | 20.35 |
| **OR** | 80–96 | 29–46 | 7.5–11 | 35–40 | 15–18 | 4.3–10.8 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 49 | 49 | 41 | 40 | 49 | 48 |
| **X̄** | 14.8 | 7.8 | 3.7 | 5.0 | 5.8 | 5.6 |
| **SD** | 0.36 | 0.23 | 0.13 | 0.16 | 0.14 | 0.16 |
| **CV** | 2.46 | 3.04 | 3.64 | 3.27 | 2.53 | 3.01 |
| **OR** | 14.0–16.0 | 7.2–8.2 | 3.4–4.0 | 4.7–5.5 | 5.4–6.2 | 5.0–5.9 |

### Description (Colour Plate II)

A small to medium-sized bat, wingspan 23–26 cm. Fur brown, similar to sympatric *M. lucifugus*, but tips of guard hairs not so glossy; dark-brown shoulder spot lacking; free edge of uropatagium bare or with only sporadic hairs. Flight membranes and ears brown. Ears long, pressed forward, extending beyond the rhinarium; tragus slender, straight and pointed. Foot relatively large, approximately half as long as tibia. Calcar slightly keeled and a little longer than free border of uropatagium. Third to fifth metacarpal approximately equal in length. Skull narrow, with relatively long rostrum, maxillary toothrow usually exceeding width across molars (M3–M3). Baculum approximately 0.9 mm long, similar to that of *M. lucifugus* (Figure 31, Table 4).

Similar Species: *M. evotis*: ears black and longer, extending 5 mm or more beyond nose when pressed forward; colour lighter with dark shoulder spots, inconspicuous fringe on free edge of uropatagium usually present. *M. keenii*: dark shoulder spots and scattered hairs on free edge of uropatagium. *M. lucifugus*: shorter ears, not extending beyond nose when pressed forward.

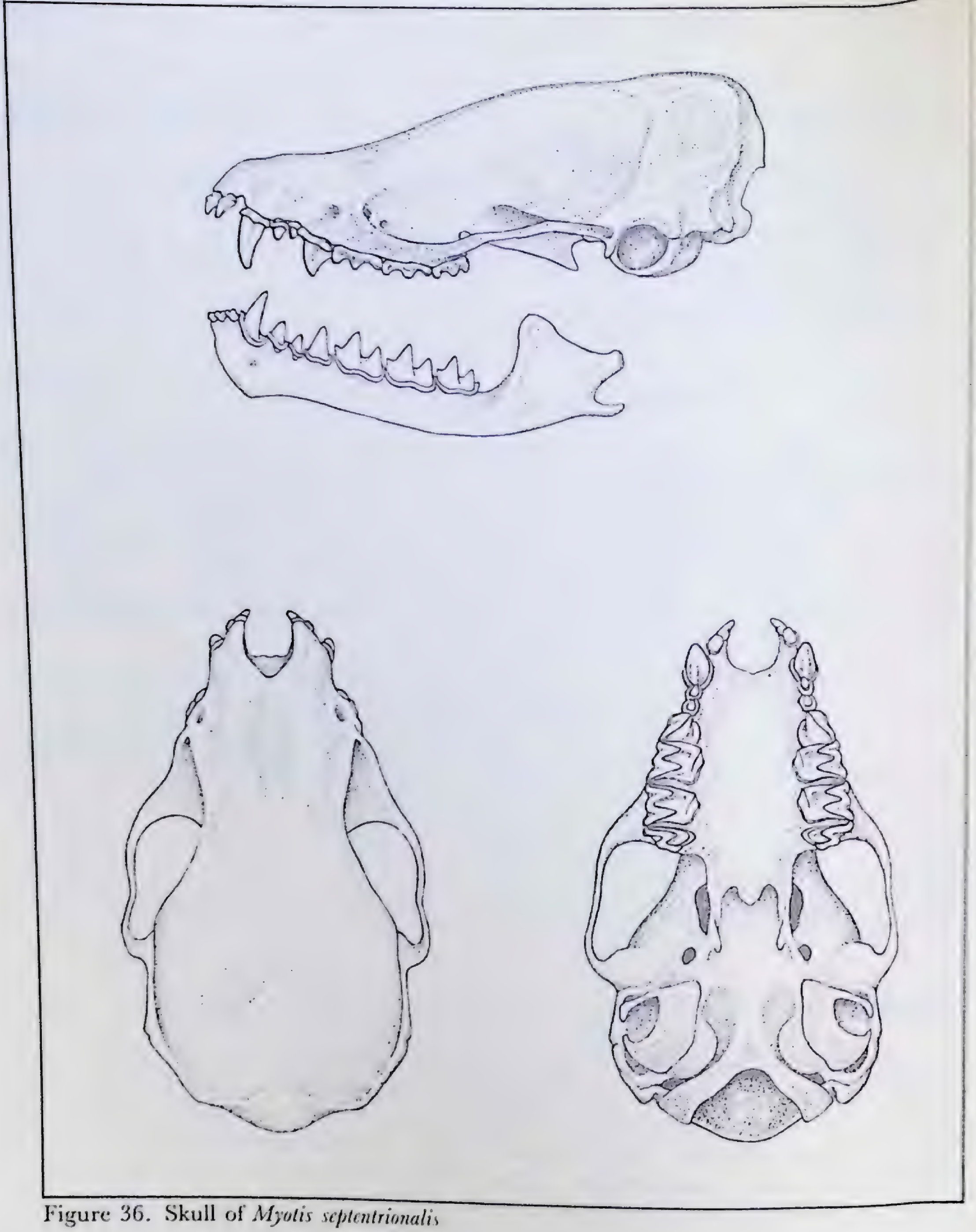
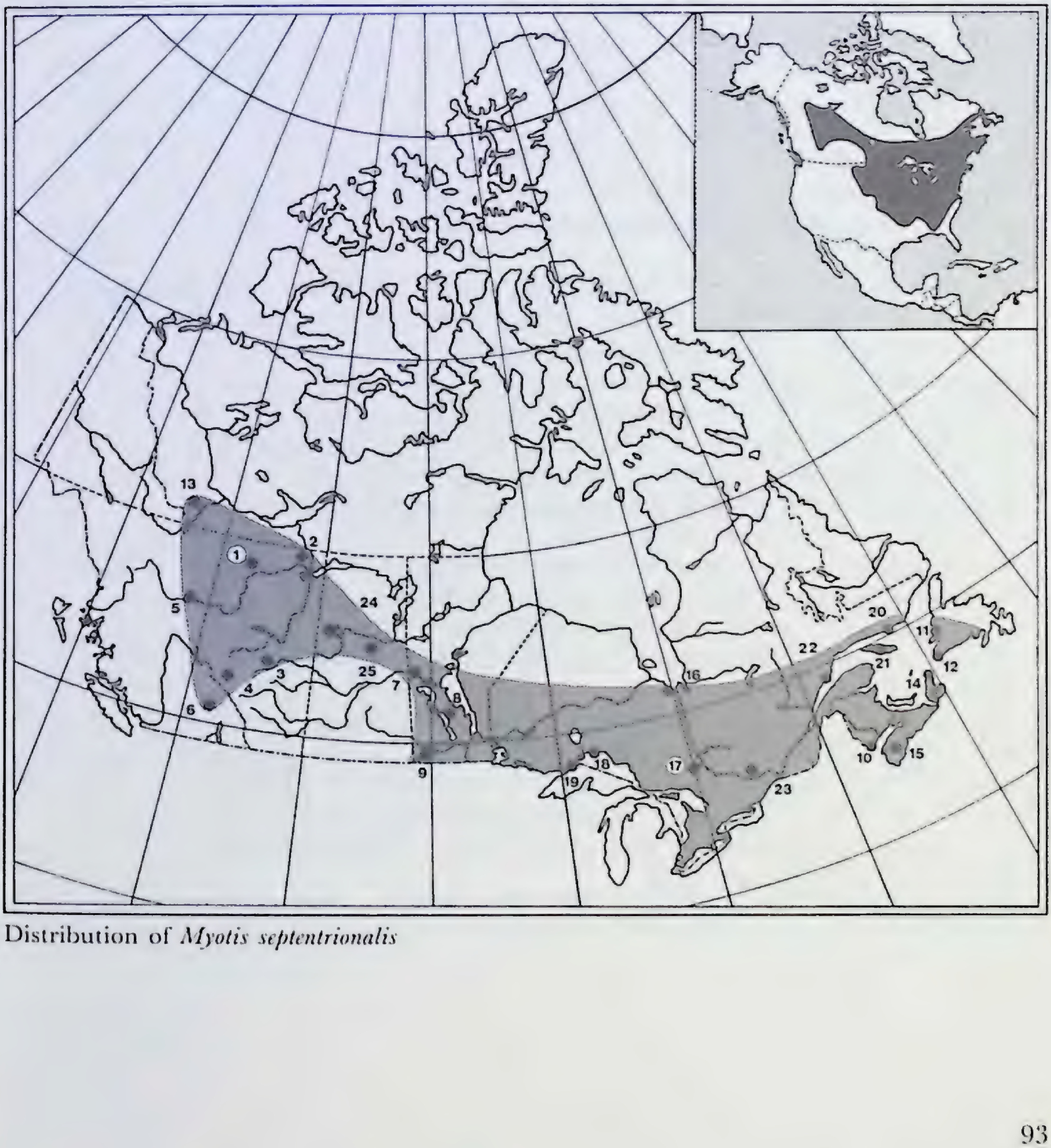


Figure 36. Skull of *Myotis septentrionalis*

## Distribution

*M. septentrionalis* is found from the Atlantic to British Columbia and north to the southern Northwest Territories. Peripheral localities: *Alberta*: (1) High Level; (2) Pine Lake, Wood Buffalo National Park; (3) Spruce Grove; (4) Cadomin Cave, near Cadomin. *British Columbia*: (5) Hudson Hope; (6) Mount Revelstoke National Park, 1 km W of Woolsey Creek. *Manitoba*: (7) The Pas; (8) Gypsumville; (9) Souris. *New Brunswick*: (10) St. Andrews. *Newfoundland*: (11) Spruce Brook; (12) Codroy. *Northwest Territories*: (13) Nahanni National Park. *Nova Scotia*: (14) Cape North; (15) Kejimkujik National Park. *Ontario*: (16) Moosonee; (17) Bear Island, Lake Timagami; (18) Jackfish; (19) Thunder Bay (Fort William). *Quebec*: (20) Natashquan; (21) Anticosti Island; (22) Godbout; (23) Laflèche Cave. *Saskatchewan*: (24) Buffalo Narrows; (25) La Ronge.

This species also occurs in the eastern United States south to northern Florida and west to a line running from eastern Oklahoma through Kansas, Nebraska, extreme northeastern Wyoming to western North Dakota.




Distribution of *Myotis septentrionalis*

## Systematics

Geographic variation in *M. septentrionalis* has not yet been analyzed over its entire range [22, 23]. No subspecies are distinguished. See also comments under *M. keenii*.

## Biology

Habitat

Little is known about the natural history of this species. It is a widespread, if not a common species, closely associated with woodlands, including the boreal forest. In summer it has been found roosting singly under loose bark of trees and occasionally behind window shutters. In winter it commonly hibernates in caves or old mines, but never in large numbers. It prefers cooler hibernation sites than *M. lucifugus* and selects narrow crevices and tight holes in areas with high humidity and may therefore be easily overlooked.

Food

Population

Analysis of the contents of the digestive tracts of a few individuals suggests that this species feeds on a variety of insects including Hemiptera, Lepidoptera, Hymenoptera, Diptera and Homoptera [24]. In Missouri, samples collected in June and early July had a preponderance of Lepidoptera in five samples (55% to 90%) and Trichoptera (60%) in one. Later, in August, samples showed a higher proportion of Coleoptera (55%) as well as Trichoptera (15%) and Lepidoptera (30%) [17]. Nothing is known about structure and dynamics of populations of this species. The maximum longevity recorded for *M. septentrionalis* is 18.5 years [11].

Activity and Behaviour

*M. septentrionalis* emerges shortly after sunset in summer. It has an initial peak of foraging activity 1 to 2 hours after sunset with a secondary peak 7 to 8 hours after sunset [15]. It forages over small woodland pools and streams, along roads and clearings within and under the forest canopy down to shrub level, 1-3 m above the ground [4, 16]. It has been observed to glean its prey from twigs [18]. This species is less gregarious than *M. lucifugus* but congregations during hibernation may sometimes number several hundred individuals [13, 14].

Reproduction

Little is known about the reproductive biology of this species in Canada, but the general pattern is probably similar to that of *M. lucifugus*. Only a few reports of maternity colonies containing up to 30 individuals have been published; the colonies were located in a barn, under shingles and loose bark [2, 3, 20]. A pregnant female with a 6 mm embryo was collected in British Columbia on 18 June [23]. In the southern part of its range (Missouri, Indiana) parturition occurs in late May to mid-June [4, 6, 7]. In New York State, females with a large embryo have been collected on 21 and 29 June and 9 July. Parturition may take place chiefly in July [12].

## References

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## *Myotis evotis* (H. Allen)
(f. Gk *eu* well; *ous* genit. *otos* ear, in reference to the well-developed ears)

**Long-eared Bat** — **Vespertilion à longues oreilles**

1864 *Vespertilio evotis* H. Allen, Monogr. Bats N. Am., Smithson. Misc. Collect. 7 (publ. 165):48
1897 *Myotis evotis* Miller, N. Am. Fauna 13:78
Type locality: Monterey, California (see Dalquest, 1943, Proc. Biol. Soc. Wash. 56:2)

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| N | 45 | 41 | 20 | 38 | 28 | 52 |
| X̄ | 93.1 | 42.5 | 8.6 | 38.6 | 19.8 | 6.7 |
| SD | 6.22 | 2.48 | 0.73 | 1.12 | 1.51 | 1.53 |
| CV | 6.69 | 5.84 | 8.39 | 2.91 | 7.69 | 22.87 |
| OR | 83–113 | 36–47 | 8–10 | 36–41 | 17–22 | 4.2–10.7 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| N | 25 | 21 | 20 | 18 | 27 | 27 |
| X̄ | 15.5 | 7.7 | 3.8 | 5.2 | 6.1 | 5.8 |
| SD | 0.33 | 0.16 | 0.10 | 0.14 | 0.17 | 0.13 |
| CV | 2.50 | 2.13 | 2.78 | 2.86 | 2.81 | 2.35 |
| OR | 14.8–16.1 | 7.4–8.2 | 3.7–4.2 | 5.0–5.5 | 5.8–6.4 | 5.5–6.0 |

### Description (Colour Plate II)

Slightly larger than other long-eared *Myotis* species: wingspan 25–29 cm. Pelage full and soft; about 10 mm long on back; colour variable, light brown to pale yellowish-brown with blackish-brown shoulder spots, free border of uropatagium with inconspicuous fringe of minute hairs. Flight membranes and ears blackish.

Ears very long, pressed forward, extending 5 mm or more beyond nose, tragus long and slender with tip bent slighty outward, a small rounded lobe at its outer base. Foot usually somewhat less than half length of tibia, calcar extending to point about halfway between foot and tip of tail, calcar usually not keeled, but sometimes with rudimentary keel ending in small lobule. Metacarpals subequal.

Skull resembles those of *M. septentrionalis* and *M. keenii*, but is somewhat larger and has larger molars [8]. Baculum resembles that of *M. keenii* and is smaller than that of *M. septentrionalis* (Figure 31, Table 4).

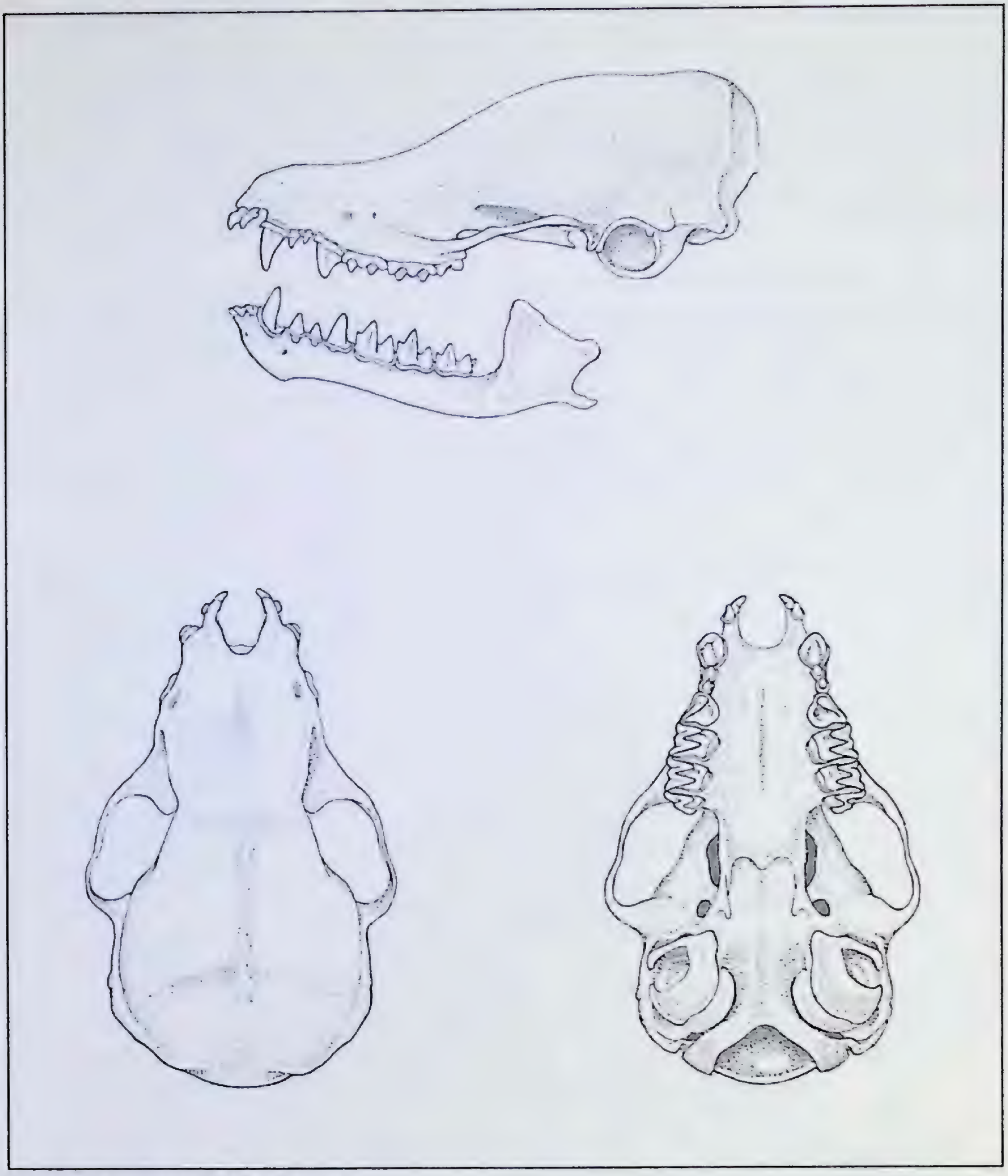

Figure 37. Skull of *Myotis evotis*

Similar Species: *M. septentrionalis*: shorter and lighter ears, extending less than 5 mm beyond nose when pressed down; no dark shoulder spots; free edge of uropatagium bare. *M. keenii*: shorter and lighter coloured ears, extending less than 5 mm beyond nose, smaller upper canine. *M. thysanodes*: usually with conspicuous dense fringe of stiff hairs on free edge of uropatagium; forearm usually over 40 mm long; ear/forearm ratio < 0.50.

### Distribution

The long-eared bat is a western species, which has not been recorded east of Saskatchewan. Peripheral localities: *Alberta*: (1) Jasper National Park; (2) Red Deer River near Rumsey. *British Columbia*: (3) Smithers; (4) Summit lake, near Prince George; (5) Victoria; (6) Parksville; (7) Kingcome Inlet; (8) Kimsquit. *Saskatchewan*: (9) Matador Field Station, near Matador; (10) 26 km S of Bengough. The species is also widely distributed in the western United States south to New Mexico, Arizona and southern California. In Mexico, the species occurs only in the peninsula of Baja California.


Distribution of *Myotis evotis*

## Systematics

Two subspecies occur in Canada, differing mainly in colour.

*M. e. evotis* (Allen), 1864, Monogr. Bats N. Am., Smithson. Misc. Collect. 7 (Publ. 165):48.
Said to be paler and somewhat larger than the next subspecies. Distribution: Eastern British Columbia, Alberta, and Saskatchewan.

*M. e. pacificus* Dalquest, 1943, Proc. Biol. Soc. Wash. 56:2.
Darker and smaller than *M. e. evotis*. Distribution: Western British Columbia and adjoining Washington.

## Biology

Habitat

The long-eared bat inhabits rocky outcroppings in coniferous forest of the Pacific coast and western mountains [2], as well as the arid badlands of Alberta and Saskatchewan, where it is found mainly along rivers. During the day this bat roosts under loose bark, in hollow trees [2] and rock crevices or fissures in clay banks. Caves are used as night roosts during the summer. Maternity colonies have been reported from buildings. There is no information on hibernation sites used by this species.

Food

No food habit studies have been done in Canada, but in the United States this bat is reported to feed primarily on beetles and moths [1, 9]. *M. evotis* may therefore be considered as a generalist, but in the southwestern United States, where it occurs together with the similar *M. auriculus*, it is reported to prey almost exclusively on beetles [4]. A case of predation by a yellow-bellied racer (*Coluber coluber mormon*) has been reported in British Columbia [6]. Nothing is known about the population structure and dynamics of this species. A longevity record of 22 years was reported for a male *M. evotis* [7].

Activity and Behaviour

The long-eared bat emerges at dusk [3]. Its flight is slow and manoeuvrable, as it forages between and within the treetops and over woodland ponds. It appears to be only moderately gregarious with maternity colonies of 13 to 30 individuals [2]. Little is known about the behaviour and reproductive biology of the species.

Reproduction

In British Columbia pregnant females, some with full-term foetuses, have been captured in late June and early July [2, 3]. In two cases one foetus was found [2].

## References


[1] Black, H.L., 1974
[2] Cowan, I. McT., and C.J. Guiguet, 1965
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[4] Husar, S.L., 1976
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[6] McIntosh, A.G.D., and P.T. Gregory, 1976
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## *Myotis thysanodes* Miller
(f. Gk *thusanos* fringe)

**Fringed Bat** | **Vespertilion à queue frangée**

1897 *Myotis thysanodes* Miller, N. Am. Fauna 13:80
Type Locality: Old Fort Tejon, Tehachapi Mountains, Kern County, California

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 4 | 4 | 4 | 4 | 4 | 4 |
| **$\bar{X}$** | 89.8 | 41.5 | 9.0 | 41.4 | 19.5 | 6.3 |
| **SD** | 2.36 | 1.91 | 0.81 | 1.37 | 0.57 | 0.66 |
| **CV** | 2.63 | 4.61 | 9.07 | 3.33 | 2.96 | 10.52 |
| **OR** | 88–93 | 40–44 | 8–10 | 40–43 | 19–20 | 5.4–7.0 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 6 | 6 | 5 | 5 | 7 | 7 |
| **$\bar{X}$** | 16.4 | 8.2 | 4.1 | 5.6 | 6.4 | 6.6 |
| **SD** | 0.34 | 0.32 | 0.24 | 0.11 | 0.16 | 0.18 |
| **CV** | 2.10 | 4.00 | 6.08 | 2.14 | 2.56 | 2.87 |
| **OR** | 16.2–17 | 7.8–8.5 | 3.9–4.4 | 5.4–5.6 | 6.2–6.6 | 6.3–6.7 |

### Description (Colour Plate II)

Resembling *M. evotis* in size and appearance, wingspan 27–30 cm. Fur not as full and long as in *M. evotis*; colour light brown on back, lacking golden tinge often present in *M. evotis*, ventral side slightly lighter; basal part of hairs blackish; free edge of uropatagium with conspicuous dorsal fringe of small stiff hairs. Ears and flight membranes blackish.

Ears relatively shorter than in *M. evotis* extending 3–5 mm beyond nose when pressed forward; external lateral edge indistinctly notched about one-third down from tip; tragus long and slender. Foot large, approximately half as long as tibia; calcar without distinct keel. Metacarpals subequal.

Skull similar to *M. evotis*; somewhat larger and broader with large teeth. Molars characterized by lack of metaloph, protoconule and paraloph (Figure 2). Baculum, dumbbell-shaped when viewed laterally, ventral surface grooved, approximately 0.7 mm long (Figure 31, Table 4).

Similar Species: *M. evotis*: longer ears, ratio of ear length to forearm length >0.50; fringe on free border of uropatagium inconspicuous, consisting of small scattered hairs.

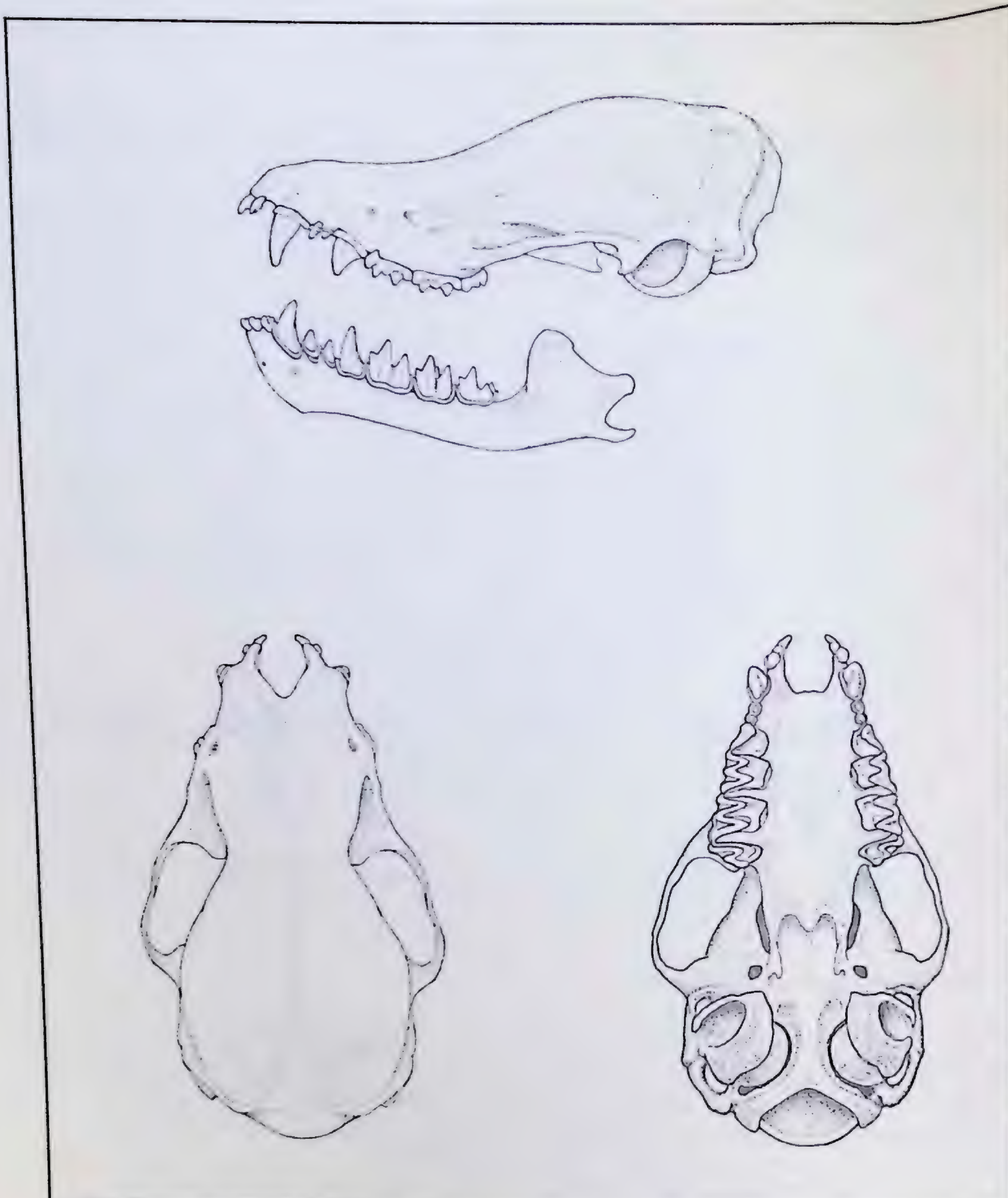

Figure 38. Skull of *Myotis thysanodes*

## Distribution

In Canada, the fringed bat is known only from the Okanagan Valley, where it was first recorded in 1937, when a maternity colony of 30 to 40 individuals was found in the attic of a house [7]. In 1979, during a survey of the bat fauna of the southern Okanagan Valley, several individuals of this species were captured at three different sites [3]. Since then more intensive field studies have shown that this species is quite common in the Okanagan Valley. Peripheral localities: *British Columbia*: **(1)** Vernon; **(2)** 4 km NW of Oliver; 10 km E of Osoyoos; and Osoyoos. South of the international border this species inhabits the western United States west of the Rocky Mountains (except for *M. t. pahasapensis*, see below) and the central highlands of Mexico south to Chiapas.


Distribution of *Myotis thysanodes*

## Systematics

Three subspecies are recognized: *M. t. thysanodes*, found over most of the species' range, *M. t. pahasapensis*, restricted to the Black Hills of South Dakota and Wyoming and *M. t. aztecus* from southern Mexico.

The fringed bat's nearest relatives are considered to be the Palearctic species *M. nattereri* and *M. pequinius* [4].

## Biology

Habitat

Very little is known about the biology of this species in Canada. In the Okanagan Valley it has been found from the open semi-desert area near Osoyoos to the dry ponderosa pine forest, at elevations of approximately 300 to 760 m respectively [3]. In the United States it is known to roost in caves, mines, rock crevices and buildings [1, 10]. Nothing is known about its habits in winter. Analyses of food habits based on small samples from New Mexico and Oregon showed that this species eats beetles, moths, harvestmen and crickets [2, 12].

Food

Population

Nothing is known about population structure and dynamics of this bat in Canada. In one population studied in New Mexico [9], nearly all females were pregnant and the sex ratio at birth was equal. Based on toothwear, the age structure was characterized by a predominance of young animals. The maximum longevity recorded for this species was 18.3 years in a male [11].

Activity and Behaviour

The fringed bat begins its nightly hunt usually between one and two hours after sunset. The flight of this species is slow (clocked at 13.8km/h in "an artificial mine tunnel" [6]) and highly manoeuvrable [5]. It is also capable of hovering flight. The flight of this species is well suited to a hunting strategy that involves gleaning as well as aerial capture of insects among branches.

Mother-infant behaviour of *M. thysanodes* has been studied in a maternity colony in New Mexico [8, 9]. Several females (guardians) stay with the young throughout the night, while the majority of females are foraging. The function of the guardians is to nurse and retrieve young. The young usually stay together in clusters separate from the adult roosts and do not show any agonistic behaviour to one another, unlike adults. If a young falls from its roost it will utter a squeaking distress call. A female will respond to the call within minutes and fly down to retrieve the young by letting it attach itself to her and returning it to the cluster. Young over two weeks old will climb the wall and return by themselves. When the young are 10 to 15 days old the females stop looking after them despite the youngs' incessant calls. Perhaps this change in maternal behaviour induces the young to fly.

Reproduction and Ontogeny

There is little information on reproduction in this species in Canada. In the southwestern United States, mating takes place in autumn and ovulation and fertilization between the end of April and mid-May. After a gestation period of 50 to 60 days the female gives birth to a single young. In New Mexico parturition occurs between 25 June and 7 July [8]. The maternity colony at

Vernon, referred to previously, contained juvenile bats on 19 July, which suggests that the period of parturition in British Columbia is similar to that reported for New Mexico.

The following information comes from studies done in New Mexico [8] and may not necessarily apply in every detail to the population in British Columbia.

The young are relatively precocial at birth averaging 54% of adult length and 22% of adult weight. The eyes are open and pinnae are erect shortly after birth. The young are pink for about one week after birth, after which the skin becomes pigmented and furred. When approximately 16.5 days old the young are capable of some flight, which is rapidly perfected so that four days later their flight is indistinguishable from that of the adults. At three weeks of age juveniles become indistinguishable from adults in size and colour but can still be distinguished by the presence of epiphysial cartilage. There is little information on the attainment of sexual maturity, but male young of the year are apparently not sexually active.

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## *Myotis californicus* (Audubon and Bachman)
(named after type locality)

**California Bat** — **Vespertilion de Californie**

1842 *Vespertilio californicus* Audubon and Bachman, J. Acad. Nat. Sci. Phila., ser. 1, vol. 8, pt. 2, p. 285
1897 *Myotis californicus* Miller, N. Am. Fauna 13:69
Type locality: California

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 27 | 27 | 30 | 21 | 22 | 19 |
| **$\bar{X}$** | 81.8 | 36.7 | 6.3 | 33.3 | 12.9 | 4.3 |
| **SD** | 4.48 | 1.93 | 0.72 | 0.83 | 1.16 | 0.58 |
| **CV** | 5.48 | 5.26 | 11.48 | 2.5 | 9.0 | 13.61 |
| **OR** | 74–95 | 34–41 | 5–8 | 32–35 | 11–15 | 3.3-5.4 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 14 | 12 | 12 | 13 | 17 | 16 |
| **$\bar{X}$** | 12.9 | 6.8 | 3.3 | 4.4 | 4.8 | 5.0 |
| **SD** | 0.40 | 0.13 | 0.07 | 0.15 | 0.15 | 0.21 |
| **CV** | 3.10 | 2.00 | 2.42 | 3.64 | 3.26 | 4.26 |
| **OR** | 12.0–13.5 | 6.6–7.0 | 3.1–3.4 | 4.2–4.8 | 4.4–5.0 | 4.6-5.3 |

### Description (Colour Plate I)

Small, wingspan 22–23 cm. Fur full and long, not glossy, varying from dull dark or blackish brown to lighter reddish-brown. Ears and flight membranes blackish. Ears relatively long, extending beyond nose when laid forward. Foot small, less than half as long as tibia (0.37–0.46); calcar less than half as long as distance from foot to tip of tail; distinct keel present. Metacarpals subequal. Skull delicate, characterized by steeply sloping forehead. Baculum gently pointed distally, broadly rounded proximally (Figure 31, Table 4).

Similar Species: In areas of sympatry (southern British Columbia), *M. ciliolabrum*: pale yellow-brown, with contrasting black snout and facial hair, bare part of snout longer than width of nostrils; skull with flatter braincase, gently sloping forehead. *M. leibii*: pelage with pronounced sheen, skull with flat braincase and gently sloping forehead; confined to the east. All other *Myotis* differ from *M. californicus* in larger size and bigger feet.

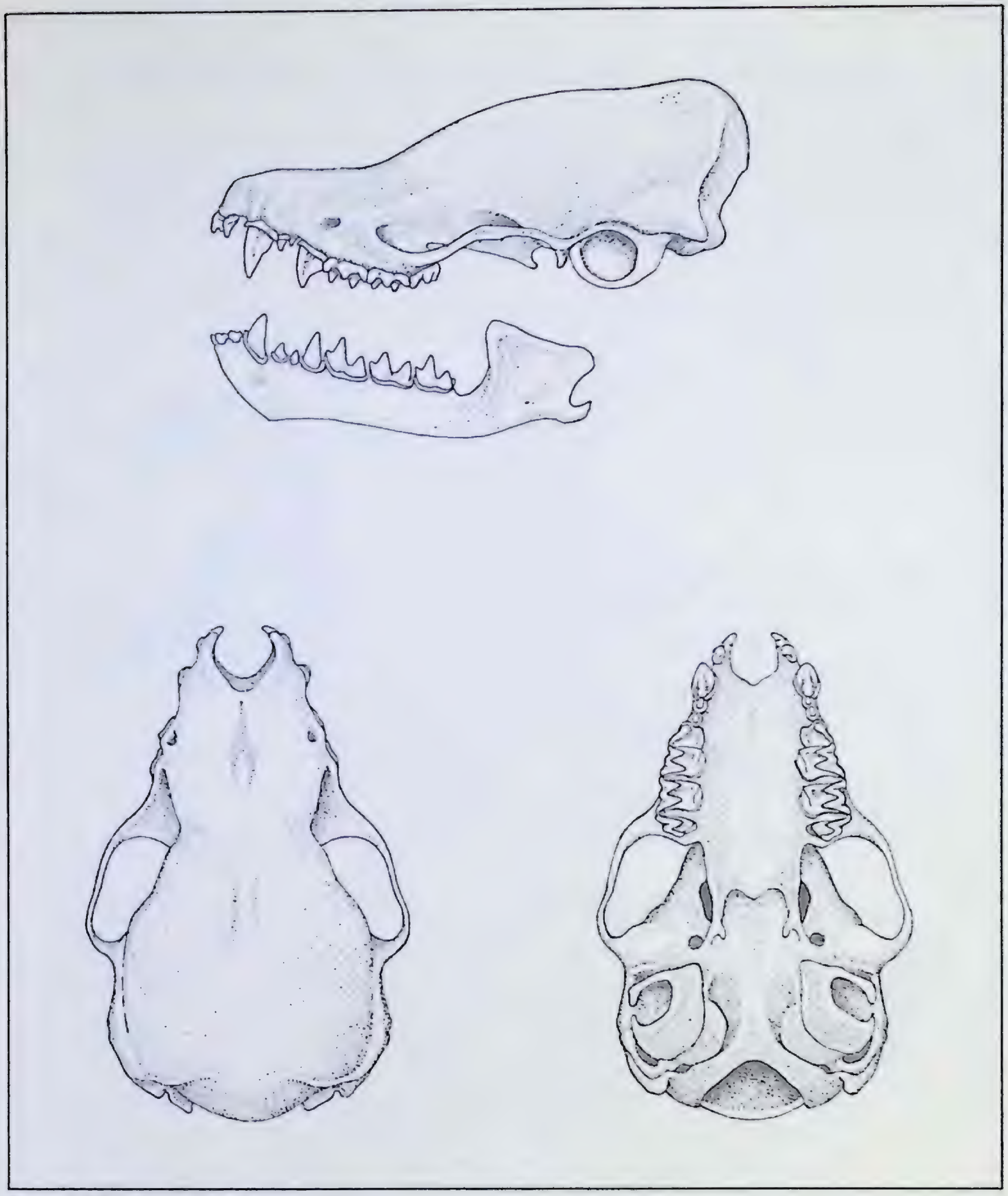

Figure 39. Skull of *Myotis californicus*

## Distribution

The Canadian distribution of this bat is confined to British Columbia, where it is common.

Peripheral localities: *British Columbia*: (1) Stuie; (2) Bute Inlet; (3) Seton Lake, near Lillooet; (4) Hemp Creek; (5) Revelstoke; (6) Wilmer National Wildlife Area, near Wilmer; (7) Nelson; (8) Victoria; (9) Burrard Inlet; (10) Alberni; (11) Cape Scott; (12) head of Rivers Inlet; (13) Skidegate; (14) Massett; (15) Langara Island.

The North American range extends from southeastern Alaska through the western United States south to southern Mexico.

Distribution of *Myotis californicus*

## Systematics

Four subspecies have been described of which only two are found in Canada.

*M. c. californicus* (Audubon and Bachman), 1842, J. Acad. Nat. Sci. Phila. ser. 1, vol. 8, pt. 2, p. 285.
A pale chestnut or hazel form. Distribution: dry interior of British Columbia.

*M. c. caurinus* (Merriam), 1895, Am. Nat. 29:860.
A dark-brown to blackish-brown form. Distribution: the humid parts of the province.

*M. californicus, M. ciliolabrum* and *M. leibii* are similar [1, 5] and presumably closely related species.

## Biology

Habitat

The California bat is found in a wide range of habitats in British Columbia, from the humid coastal forest to semidesert, and from sea level to elevations of at least 1800 m. In arid areas it is usually found in the vicinity of water. Selection of roosting sites is equally variable and includes buildings, rock crevices, hollow trees, and spaces under loose bark [4]. Small numbers of hibernating individuals have been reported from mines and caves.

Food

California bats feed on small flying insects, chiefly flies and small moths as well as on small beetles and some other insects [6]. In the Okanagan Valley this species fed on Diptera and Trichoptera more than on Lepidoptera or Coleoptera [7].

Activity and Behaviour

Individuals of this species emerge shortly after sunset returning to night roosts after filling their stomachs [4, 7]. There are two activity peaks, one between 22:00 and 23:00, the other between 01:00 and 02:00 [7]. Foraging continues until dawn. Its flight is slow and erratic and it hunts low near vegetation, preferably near or over water close to shore [7], usually between 1 and 3 m above the surface. It detects prey at close range ($<1$ m) [3]. Its feeding strategy consists of locating and feeding in concentrations of insects where its slow manoeuvrable flight allows it to capture several insects in quick succession over a short distance [3].

The sexes roost separately during the summer when the females form small maternity colonies, but mingle from September to March.

Reproduction and Ontogeny

Little is known about reproduction and ontogeny in *M. californicus*. Breeding takes place in autumn and the female gives birth to a single young in July [2].

**References**

[1] Bogan, M.A., 1974
[2] Cowan, I. McT., and C.J. Guiguet, 1965
[3] Fenton, M.B., and G.P. Bell, 1979
[4] Krutzsch, P.H., 1954
[5] van Zyll de Jong, C.G., in press
[6] Whitaker, J.O., Jr., C. Maser, and L.E. Keller, 1977
[7] Woodsworth, G.C., 1981

## *Myotis ciliolabrum* (Merriam)

(f. L *cilium* eyelid; *labrum* lip, whiskered lip)

**Western Small-footed Bat** | **Vespertilion pygmée de l'Ouest**

1886 *Vespertilio ciliolabrum* Merriam, Proc. Biol. Soc. Wash. 4:2
1928 *Myotis subulatus* Miller and Allen, Smithson. Inst., U.S. Nat. Mus. Bull. 144, p. 104
1968 *Myotis leibii* Glass and Baker, Proc. Biol. Soc. 81:257–60
Type locality: near Banner, Trego County, Kansas

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 52 | 52 | 22 | 50 | 19 | 50 |
| **$\bar{X}$** | 84.9 | 39.2 | 6.5 | 32.2 | 13.8 | 4.9 |
| **SD** | 3.78 | 2.71 | 0.51 | 0.68 | 0.75 | 1.06 |
| **CV** | 4.46 | 6.91 | 7.79 | 2.11 | 5.47 | 21.61 |
| **OR** | 76–90 | 31–43 | 6–7 | 30–33 | 13–15 | 2.8–7.1 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 40 | 40 | 40 | 40 | 40 | 40 |
| **$\bar{X}$** | 13.7 | 7.0 | 3.2 | 4.5 | 5.2 | 5.3 |
| **SD** | 0.33 | 0.14 | 0.10 | 0.16 | 0.16 | 0.17 |
| **CV** | 2.41 | 2.00 | 3.12 | 3.56 | 3.08 | 3.21 |
| **OR** | 13.0–14.5 | 6.8–7.4 | 3.0–3.5 | 4.1–4.7 | 4.8–5.5 | 5.0–5.6 |

### Description (Colour Plate I)

Size small; wingspan 21–25 cm. Fur dense and long, lacking any pronounced sheen; colour varies from pale yellow-brown to flaxen on the back, and from buff to nearly white ventrally. Flight membranes, ears and face contrasting black. Ears relatively long, reaching or exceeding tip of nose when laid forward; tragus slender, tapering, about half as long as ear. Foot small, less than half as long as tibia, calcar with distinct keel. Metacarpals subequal. Skull small, forehead gently sloping, braincase higher than in *M. leibii*, lambdoidal and sagittal crests confluent and more prominent than in that species. Baculum saddle-shaped, concave ventrally 0.6–0.9 mm long (Figure 31, Table 4).

Similar Species: Sympatric *M. californicus*: dark or reddish-brown fur, without contrasting black snout and facial hair; bare part of snout about as long as width of nostrils in dorsal aspect (Figure 17); skull with more steeply sloping forehead. *M. leibii*: eastern, fur with pronounced golden sheen dorsally, skull with flatter cranium.

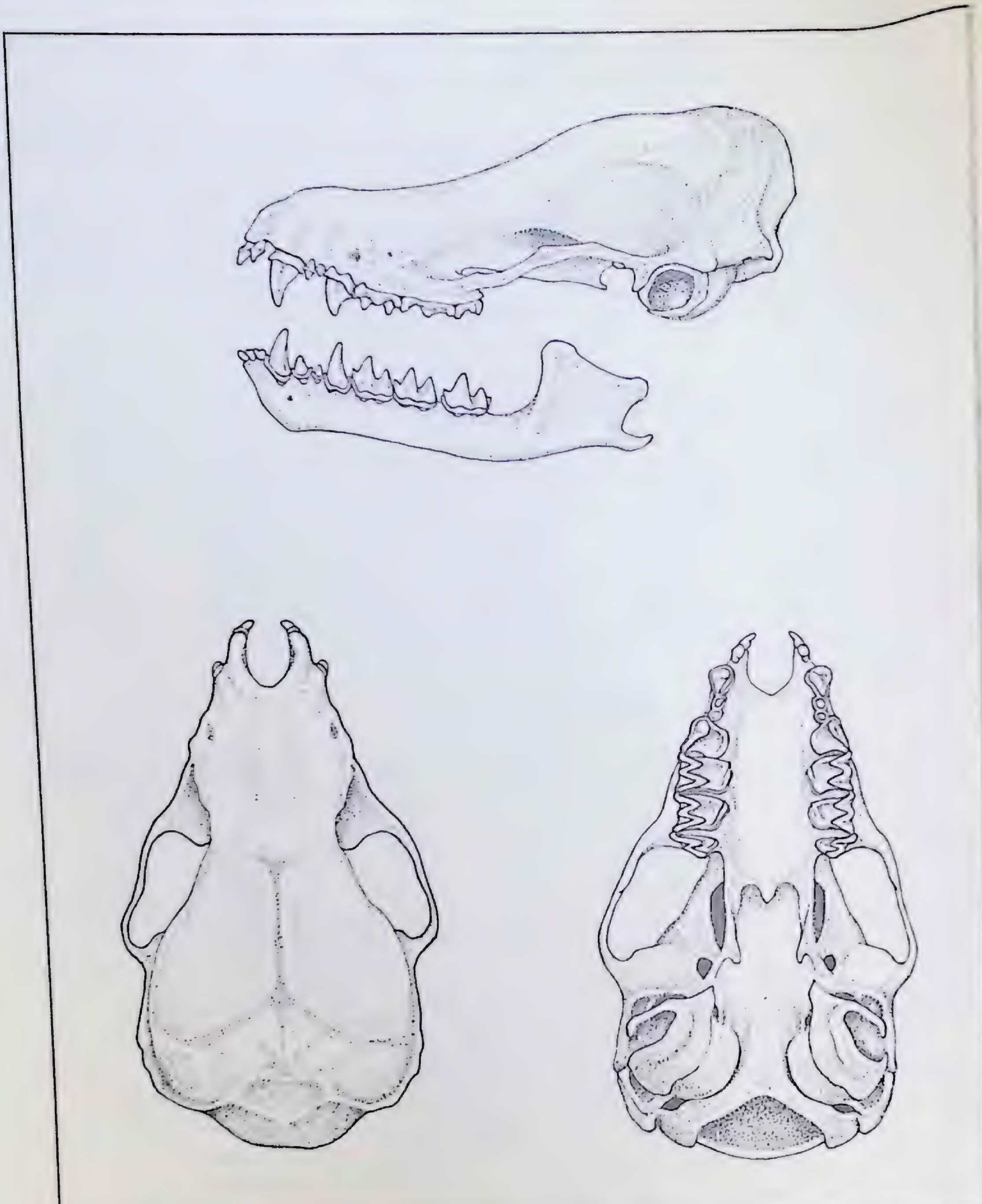

Figure 40. Skull of *Myotis ciliolabrum*

## Distribution

The western small-footed bat inhabits the arid regions of western Canada, the short-grass prairies of Alberta and Saskatchewan and the Similkameen and Okanagan valleys of southern British Columbia. Peripheral localities: *Alberta:* (1) Red Deer River, near Rumsey; (2) Little Sandhill Creek at Red Deer River; (3) Lethbridge. *British Columbia:* (4) Oyama; (5) Keremeos; (6) Osoyoos Lake. *Saskatchewan*: (7) South Saskatchewan River, north of Stewart Valley.

South of our border, the species is found throughout the western United States, excepting the humid coastal areas, and south into Mexico.


Distribution of *Myotis ciliolabrum*

## Systematics

Two subspecies are recognized, based on the colour of the pelage. Both occur in Canada.

*M. c. ciliolabrum* (Merriam) 1886, Proc. Biol. Soc. Wash. 2:2.
A pallid form, flaxen above, nearly white below. Distribution in Canada: Alberta and Saskatchewan.

*M. c. melanorhinus* (Merriam) 1890, N. Am. Fauna 3:46.
A rich yellowish-brown form with buff underparts. Distribution in Canada: Similkameen and Okanagan valleys of southern British Columbia.

Specimens of *M. c. ciliolabrum* from Alberta have somewhat larger cranial measurements than those of *M. c. melanorhinus* from British Coumbia (SL $\bar{x} = 13.7$; SD = 0.34; $\bar{x} = 13.4$; SD = 0.20; MW $\bar{x} = 7.1$; SD = 0.14; $\bar{x} = 6.9$; SD = 0.10; IOW $\bar{x} = 3.2$; SD = 0.10; $\bar{x} = 3.1$; SD = 0.08; CD $\bar{x} = 4.5$; SD = 0.12; $\bar{x} = 4.3$; SD = 0.12 respectively). However, *M. c. melanorhinus* from the American Southwest are larger (SL $\bar{x} = 13.9$) than those from Canada and size can therefore not be regarded as a diagnostic character for distinguishing the two subspecies.

*M. c. ciliolabrum* and *M. c. melanorhinus* were until recently regarded as subspecies of *M. leibii*. However, morphometric [11] and biochemical [5] evidence has demonstrated that this view is no longer tenable. Multivariate craniometric comparisons show that *M. ciliolabrum* and *M. leibii* are as distinct from one another as each is from the other member of the *leibii* group, *M. californicus*. Specimens from the alleged zone of intergradation between the eastern and western small-footed bats in Oklahoma [3, 4] did not show any evidence of intermediacy. To the contrary, they could be assigned unequivocally to either the western (*M. ciliolabrum*) or eastern form (*M. leibii*) [11]. Electrophoretic comparison of *M. c. melanorhinus* and *M. leibii* [5] showed differences greater than expected between subspecies of one species and as great as those observed between some species of bats and rodents, thus confirming the morphometric evidence.

## Biology

Habitat

*M. ciliolabrum* appears to prefer arid habitats where it is associated with cliffs, talus and, in the prairies, with clay buttes and steep riverbanks [5, 6, 7]. It roosts in crevices in rock faces and clay banks [1, 10] and it may use the spaces beneath and between boulders in talus. The species has also been found roosting beneath bark and in a barn [6]. For hibernation it selects caves and mines but no data are available for Canada.

Food

Information on food habits suggests that *M. ciliolabrum* feeds on a variety of small insects. Two stomachs from Montana contained small Diptera, Coleoptera, Cicadellids and Trichoptera [7]. In Oregon [12] this species fed predominantly on Lepidoptera, Hemiptera and Diptera. In the Okanagan Valley in British Columbia, Trichoptera predominated [13].

Activity and Behaviour

The western small-footed bat begins its nightly activity at dusk shortly after sunset with peaks of activity between 22:00 and 23:00 hrs and 01:00 and 02:00 hrs [13]. It flies slowly and errat-

ically as it forages at heights of 1 to 3 m along cliffs and rocky slopes, unlike the similar sympatric *M. californicus*, which prefers to hunt over and near water. In the Okanagan Valley the proportions of different prey species taken by *M. ciliolabrum* and *M. californicus* are similar [13]. It appears, therefore, that these two highly similar species co-exist by spatial partitioning of the available food resource. Information on reproduction is sparse. Observations of pregnant and lactating females suggest that parturition takes place in late June and early June [2,7]. There is no information on litter size in Canada. In the United States, one young appears to be the rule, but twins occur [7, 10].

Reproduction and Ontogeny

**References**


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[8] Robbins, L.W., M.D. Engstrom, R.B. Wilhelm, and J.R. Choate, 1977
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[10] Tuttle, M.D., and L.R. Heaney, 1974
[11] van Zyll de Jong, C.G., in press
[12] Whitaker, J.O., Jr., C. Maser, and S.P. Cross, 1981
[13] Woodsworth, G.C., 1981

## *Myotis leibii* (Audubon and Bachman)
(Named after collector, Dr. G.C. Leib)

**Eastern Small-footed Bat** — Vespertilion pygmée de l'E

1842 *Vespertilio leibii* Audubon and Bachman, J. Acad. Nat. Sci. Phila., ser. 1, vol. 8, pt. 2, p. 284
1928 *Myotis subulatus* Miller and Allen, Smithson. Inst., U.S. Nat. Mus. Bull. 144, p. 104
1968 *Myotis leibii* Glass and Baker, Proc. Biol. Soc. Wash. 81:257-60
Type locality: Erie County, Ohio

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| N | 40 | 40 | 40 | 30 | 35 | 7 |
| $\bar{X}$ | 82.6 | 36.2 | 7.4 | 32.2 | 12.5 | 3.8 |
| SD | 4.05 | 2.18 | 0.81 | 0.78 | 0.99 | 0.80 |
| CV | 4.90 | 6.03 | 10.9 | 2.44 | 7.90 | 21.05 |
| OR | 74–93 | 30–40 | 6–8.5 | 30–34 | 11–14 | 3.2–5.5 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| N | 36 | 36 | 36 | 36 | 36 | 36 |
| $\bar{X}$ | 13.5 | 7.1 | 3.3 | 4.2 | 5.1 | 5.2 |
| SD | 0.28 | 0.18 | 0.10 | 0.12 | 0.12 | 0.13 |
| CV | 2.07 | 2.84 | 3.97 | 3.91 | 3.13 | 2.8 |
| OR | 13–14.1 | 6.4–7.4 | 3.1–3.6 | 4.0–4.4 | 4.8–5.2 | 4.9–5.4 |

### Description (Colour Plate I)

Size small, wingspan 21–25 cm. Fur full, silky and glossy brown, shiny tips of longer hairs give the pelage a golden sheen, ears and flight membranes blackish. Ears relatively long, reaching or exceeding tip of nose when laid forward; tragus slender, tapering, about half as long as ear. Foot small, less than half as long as tibia; calcar about as long as free border of uropatagium, with prominent keel. Metacarpals subequal. Skull small, braincase flat, forehead gently sloping. Baculum somewhat saddle-shaped, concave ventrally and with dorsal prominence (Figure 31, Table 4).

Similar Species: *M. californicus*: western, fur dull, dark-brown or reddish-brown without contrasting black snout and facial hair; skull with rounded braincase, steeply sloping forehead. *M. ciliolabrum*: western, paler in colour, lacking pronounced sheen; braincase vaulted, I3I3W relatively narrower (Figure 25). Other *Myotis*, larger with bigger feet.

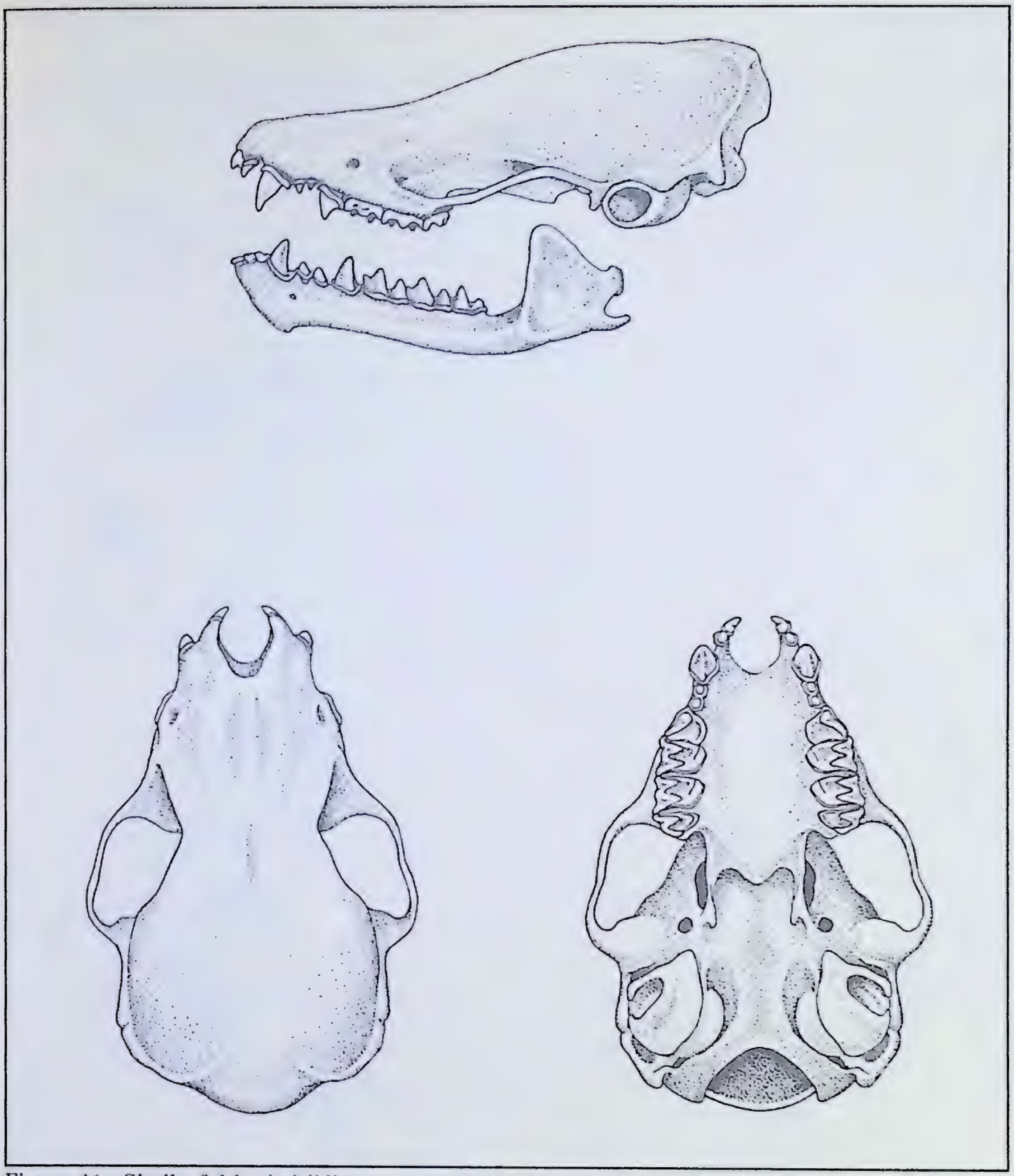

Figure 41. Skull of *Myotis leibii*

## Distribution

The eastern small-footed bat occurs in the Deciduous and Great Lakes–St Lawrence forest region of Ontario and southern Quebec, west to the shore of Lake Superior. *Ontario*: (1) Lake Superior Provincial Park; (2) Webbwood; (3) Mount Brydges. *Quebec*: (4) Laflèche Cave.

In the United States, the species' distribution is centred in the Appalachians from western New England south to extreme northern Georgia with scattered populations to the west in Kentucky, Missouri, Arkansas and Oklahoma.


Distribution of *Myotis leibii*

## Systematics

No subspecies are recognized. For comments on the systematic relationships with *M. ciliolabrum*, see the discussion under that species (p. 114).

## Biology

Habitat

The habitat requirements of this species are poorly known. In summer it has been found sparingly in buildings [1,7], beneath rock slabs [12] and under a stone [1]. In winter the only known hibernation sites are caves and old mines [2, 3, 5, 6, 10], where it often occupies narrow crevices, or hangs on the wall or from the ceiling. It has also occasionally been found on the floor of the hibernaculum under rocks [2, 9].

This small bat is very hardy, entering hibernation late and leaving the hibernacula early (late November and early April respectively in eastern Ontario) [3]. It tolerates colder temperatures than *M. lucifugus*, arousing from torpidity below -9°C, compared to -4°C in *M. lucifugus* [3]. This tolerance is reflected in its selection of sites nearer the entrance of the hibernaculum where humidity and temperatures are lower and subject to greater fluctuation. Weight loss during hibernation from December to April in a combined sample of males and females was from an average of 5.6 g to 4.7 g or 16% [3].

Food

There is no information of food habits.

Population

Relative to other species of bats in its distributional range, *M.leibii* is an uncommon bat. The reasons for the relative rarity are not understood. The sex ratio of hibernating populations of *M. leibii* shows nearly equal numbers of males and females, and a longevity of 12 years has been reported for a female [11]. In Ontario, the rate of survival for females was found to be considerably lower than that of males (estimated mean annual survival of 0.421 and 0.757 respectively) [8]. The lower female survival in northern populations may be a result of a combination of factors: the greater demands of reproduction on females; higher metabolic rates and longer sustained activity during the day in summer (i.e. less time spent in daytime lethargy); and greater exposure to possible disease-carrying ectoparasites in maternity colonies [8]. The uncommon status of *M. leibii* in eastern Canada could be a result of low survival and probably a small litter size. Aside from this meagre information, nothing is known about the structure and dynamics of *M. leibii* populations.

Activity and Behaviour

The eastern small-footed bat emerges at dusk shortly after sunset. It flies slowly and erratically, usually at heights between 1 and 3 m. Two *M. leibii* were found in Ontario approximately 16 and 19 km from the hibernaculum where they were banded [7], suggesting that this species may hibernate not far from its summer range.

Reproduction and Ontogeny

Information on reproduction is largely lacking. A small maternity colony of about a dozen bats was found behind a sliding barn door in Ontario in early July [7].

## References

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## Genus *Pipistrellus* Kaup, 1829
(f. Italian *pipistrello, vispitrello,* diminutive of *vespertilio* bat)

*Pipistrellus* is characterized by a dental formula of i2/3; c1/1; p2/2; m3/3; possessing one small premolar less in the upper and lower jaw than *Myotis*. The rostrum is shorter than in *Myotis*, the ears usually smaller and broader, the tragus blunter. On the whole the genus lacks striking specializations. The species in the genus vary in size, and include some of the smallest and largest vespertilionids.

Two North American species are currently assigned to the genus. There are about 47 species in the world, mainly in Eurasia, Africa and Australia. The genus has nearly as much chromosomal diversity as the rest of the Vespertilionidae combined, and our only species (*P. subflavus*) appears to be related to *Myotis* on the basis of chromosomal banding [1].* In some morphological characters *Pipistrellus*, on the other hand, resembles *Eptesicus* and *Nyctalus*, and the boundaries between these genera are at the moment diffuse and ill-defined. *Pipistrellus* may represent a central vespertilionid group, from which other lineages have been derived. A taxonomic revision of the genus is needed.

### References

[1] Bickham, J.W., 1979
[2] Hall, E.R., and W.W. Dalquest, 1950
[3] Miller, G.S., Jr., 1897*a*

*Recent morphological evidence confirms the relationship to *Myotis*. On the basis of the morphology of its dentition, distal part of the humerus and baculum, Menu (1984 Mammalia 48(3): 409–16) removed *subflavus* from *Pipistrellus* and placed it in *Perimyotis* nov. gen. to indicate its affinity to the Myotini.

## *Pipistrellus subflavus* (F. Cuvier)

(f. L *sub* under; *flavus* yellow, i.e. somewhat yellow)

**Eastern Pipistrelle** — **Pipistrelle de l'Est**

1832 *V* [*espertilio*] *subflavus* F. Cuvier, Nouv. Ann. Mus. Hist. Nat. Paris 1:17
1897 *Pipistrellus subflavus* Miller, N. Am. Fauna 13:90
Type locality: Eastern United States, probably Georgia

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 28 | 28 | 21 | 12 | 16 | 7 |
| **$\bar{X}$** | 84.5 | 38.3 | 9.2 | 33.7 | 12.5 | 6.9 |
| **SD** | 5.32 | 3.26 | 0.79 | 1.11 | 1.09 | 0.69 |
| **CV** | 6.31 | 8.51 | 8.68 | 3.29 | 8.77 | 10.18 |
| **OR** | 74–98 | 30–46 | 8–10.5 | 32–36 | 11–14.5 | 6–7.9 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 30 | 29 | 31 | 31 | 30 | 30 |
| **$\bar{X}$** | 12.9 | 6.8 | 3.6 | 4.8 | 4.2 | 5.2 |
| **SD** | 0.25 | 0.20 | 0.12 | 0.33 | 0.12 | 0.16 |
| **CV** | 1.99 | 3.07 | 3.47 | 7.04 | 2.92 | 3.24 |
| **OR** | 12.3–13.3 | 6.4–7.2 | 3.4–3.6 | 3.8–5.8 | 3.8–4.4 | 4.8–5.5 |

### Description (Colour Plate I)

Size small, wingspan 20–26 cm. Fur tricoloured, base of hairs dark grey, middle section yellowish brown, tips brown; overall colour varying from yellowish or orangish-brown to greyish-brown, dark brown or nearly black; dorsum and venter nearly same colour, not contrasting. Juvenile pelage darker than adult. Flight membranes blackish, but skin on forearm, and to a lesser extent on metacarpals, contrastingly lighter, pinkish or reddish-brown; naked parts of snout and ears pale brown. Ears extending slightly beyond nose when pressed forward, tragus short, straight, tapering to rounded tip. Foot large, more than half as long as tibia, dorsal surface of foot and toes covered whith conspicuous light brown hairs; calcar not keeled, exceeding tibia in length. Third, fourth and fifth metacarpals subequal; thumb relatively long (approximately 20% of forearm length). Skull small, with short, broad rostrum. Baculum Y-shaped (Figure 31, Table 4).

Similar Species: This bat can be distinguished from all other small bats in its range by its tricoloured fur and the presence of one small premolar in the upper and lower jaw.

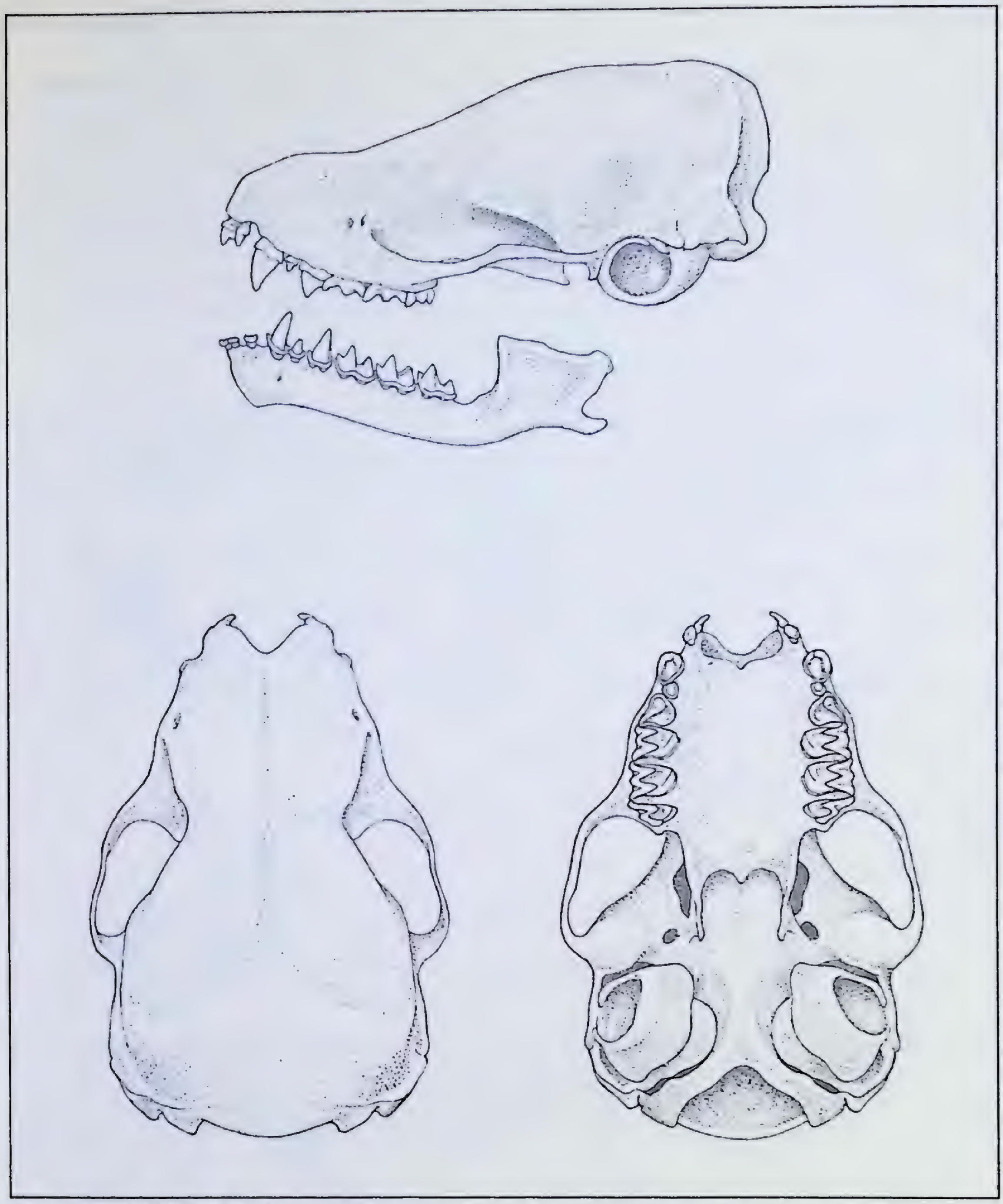

Figure 42. Skull of *Pipistrellus subflavus*

## Distribution

The eastern pipistrelle's distribution in Canada is restricted to southeastern Canada. Since this is at the northern limit of its range, this species is not abundant here.

Peripheral localities: *New Brunswick*: (1) Turtle Creek Cave, near town of Turtle Creek. *Nova Scotia:* (2) Gays River Gold Mines, near town of Gays River; (3) Grafton Lake. *Ontario:* (4) Fourth Chute near Douglas; (5) Rockwood. *Quebec*: (6) Gracefield; (7) Joliette.

In the eastern United States the eastern pipistrelle is a widely distributed and common bat. The species' range extends south to the Gulf of Mexico, eastern Mexico and as far south as Honduras.


Distribution of *Pipistrellus subflavus*

## Systematics

Four subspecies of the eastern pipistrelle are recognized, of which only one is found in Canada, *P.s. subflavus* [4].

The two species of pipistrelles found in North America, *P. subflavus* and *P. hesperus*, differ from one another in some important respects and may not be as closely related as their inclusion in the same genus suggests. There are significant differences in the karyotypes of the two species [1]. (*P. subflavus*: 2N = 30; FN = 56; autosomes 14M and SM; X chromosome SM; Y chromosome A; *P. hesperus*: 2N = 28; FN = 46; autosomes 10M and SM and 3A; X chromosome SM; Y chromosome A.) These differences appear to be significant in view of the remarkable conservative nature of the karyotype at the generic level in other North American vespertilionids. Analysis of chromosomal banding in *P. subflavus* suggests that it has affinities with the *Myotis* group [3]. The differences in the bacula of *P. subflavus* and *P. hesperus* are also striking. In *P. subflavus* the baculum is a small (approximately 0.6 mm long) Y-shaped bone, with the two prongs in a proximal position (Figure 31); whereas *P. hesperus* has a much larger (2 mm or more) and very differently shaped baculum [12]. Not only do the two New World pipistrelles differ significantly from one another, both differ also significantly from the type species *P. pipistrellus* and other European species of the genus with respect to karyotype and bacular morphology. These differences are possibly important enough to warrant generic or subgeneric distinction and point out the need for a comprehensive review of *Pipistrellus* and related genera.

## Biology

Habitat

This bat inhabits open country with large trees and also the edges of woodlands [7]. It probably roosts in the foliage of trees [8] and, although maternity colonies in a garage and barn have been reported (Fenton, pers. comm.), it appears to be rarely found in buildings. For hibernation, the eastern pipistrelle uses caves and mines [10, 11], where it selects warmer locations than other species. It is also known to use smaller caves than other bats.

Food

The food habits of the eastern pipistrelle in Canada are not well known, but in the United States analyses of the contents of digestive tracts of this species revealed that it feeds on a variety of small insects comprising Homoptera, Coleoptera, Diptera and Hymenoptera [15, 17].

Population

Because of the relative rarity of this bat here, there is no information on population structure and dynamics in Canada. Information from the United States suggests general similarity to *M. lucifugus* in that males outnumber females at least in parts of the range, and there is low survival of young bats, with increasing survival rates to 3.5 years followed by a decreasing survival rate as the maximum life span is approached (approximately 9 years for females, 14 to 15 for males) [6, 16].

Activity and Behaviour

The eastern pipistrelle emerges from its day roost early, at about sunset. It has intermittent feeding periods to midnight and another period of feeding activity toward dawn. It flies slowly and erratically as it forages back and forth over small areas near trees or over water. This bat appears to feed alone, although in

late summer several (up to four or five) may be seen hunting together.

There is little information on the reproduction of this species in Canada. Information from the United States suggests a reproductive cycle similar to that of other small temperate zone bats, with June and July as the probable period of parturition in our latitudes [18]. Litter size is usually two. The young are large (weighing as much as one-fourth of the mother's weight) [13] and develop rapidly, being able to fly within a month after birth [2]. They probably do not mate in their first year.

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## Genus *Lasionycteris* Peter, 1865
(f. Gk *lasios* hairy; *nukteris* bat)

A monotypic genus characterized by short ears, which are nearly as long as broad with a short, straight round-tipped tragus, blackish or dark-brown fur, sprinkled with white-tipped hairs, extending halfway down the uropatagium. Wing membranes and ears black. Skull with nearly straight dorsal profile and broad, short rostrum. Dental formula i2/3; c1/1; p2/3; m3/3. The baculum of this genus is very different from that of other North American vespertilionids, in being large (nearly 3 mm), having a swollen base, tapering gradually to the middle of the cylindrical shaft and enlarging slightly at the tip (Figure 31, Table 4). The karyotype is also most divergent from that of other North American vespertilionids (2N = 20; FN = 28, with autosomes 5M and SM, 4A; X chromosome SM; Y chromosome A) [1, 2]. The genus, which is restricted to North America, is rather distinct from other American vespertilionids, but chromosomal banding analysis suggests affinities with the *Myotis*-like group of vespertilionids [2].

**References**

[1] Baker, R.J., and J.L. Patton, 1967
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[3] Hamilton, W.J., Jr., 1949
[4] Miller, G.S., Jr., 1897*a*

## *Lasionycteris noctivagans* (Le Conte)
(f. L *nox* genit. *noctis*
night; *vagus* wandering)

**Silver-haired Bat** **Chauve-souris argentée**

1831 *Vespertilio noctivagans* Le Conte, *in* McMurtrie's Animal Kingdom... vol. 1, p. 31
1865 *Lasionycteris noctivagans* Peters, Akad. Wiss. Berl., p. 648
Type locality: Eastern United States

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 33 | 33 | 31 | 8 | 8 | 9 |
| **$\bar{X}$** | 97.0 | 39.3 | 9.0 | 41.9 | 15.8 | 11.0 |
| **SD** | 7.51 | 4.73 | 1.37 | 2.80 | 0.22 | 2.28 |
| **CV** | 7.74 | 12.04 | 15.19 | 6.68 | 1.43 | 20.77 |
| **OR** | 80–113 | 25–48 | 7–12 | 36–45 | 15–16 | 9.1–16.7 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 23 | 17 | 25 | 21 | 25 | 23 |
| **$\bar{X}$** | 15.7 | 8.4 | 4.2 | 5.0 | 5.8 | 6.6 |
| **SD** | 0.42 | 0.28 | 0.13 | 0.15 | 0.16 | 0.16 |
| **CV** | 2.68 | 3.35 | 3.34 | 3.20 | 2.88 | 2.48 |
| **OR** | 15–16.5 | 7.9–8.8 | 4–4.5 | 4.6–5.2 | 5.4–6.0 | 6.2–6.9 |

### Description (Colour Plate I)

Size medium; wingspan 27–31 cm. See description of genus. Similar species: *Lasiurus cinereus*: larger, dorsal side of uropatagium heavily furred, so that membrane cannot be seen.

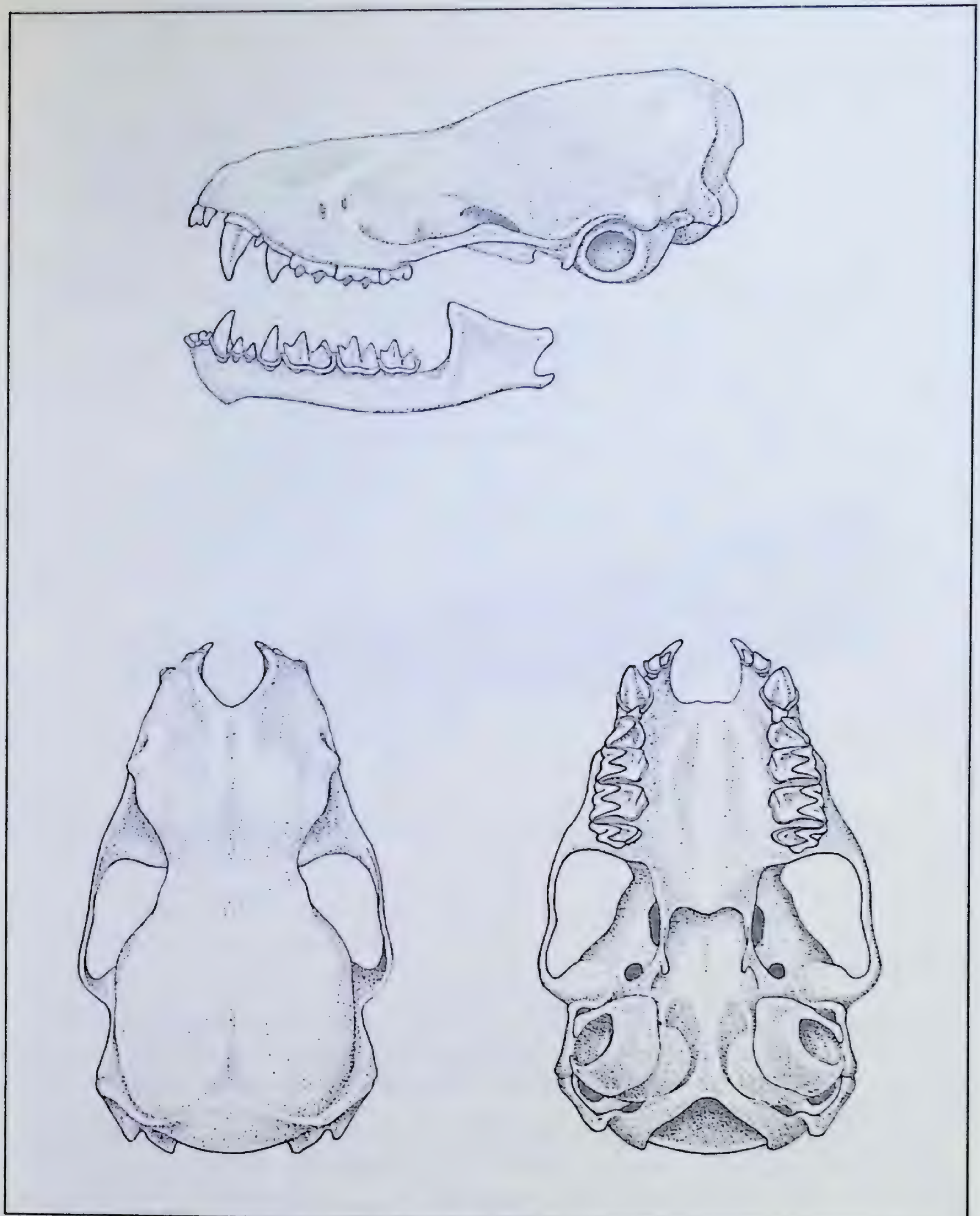

Figure 43. Skull of *Lasionycteris noctivagans*

Distribution of *Lasionycteris noctivagans*

## Distribution

This species is widely distributed in Canada in summer and is one of the most common bats in the aspen parklands of the prairie provinces. In winter, this largely migratory species has been found only in southwestern British Columbia [4, 18].

Peripheral localities: *Alberta*: (1) 46.5 km N of Hotchkiss. *British Columbia*: (2) Tatlatui Lake; (3) Charlie Lake; (4) Sayward; (5) Masset. *Manitoba*: (6) Reader Lake near The Pas; (7) Gypsumville. *New Brunswick*: (8) Fredericton. *Nova Scotia*: (9) Lake Kejimkujik. *Ontario*: (10) Moose Factory. *Quebec*: (11) Camp Dorval, Hwy. 58, Parc de la Vérendrye; (12) Mont-Saint-Hilaire. *Saskatchewan*: (13) Frobisher Lake.

The species is also found over most of the United States. It winters in the United States mainly south of latitude 42°N, but on the Pacific Coast with its mild climate as far north as British Columbia [7, 8, 18].

## Systematics

The silver-haired bat is a monotypic species showing little or no geographic variation. See account of genus for comments on relationships to other vespertilionids.

## Biology

Habitat

In summer the silver-haired bat inhabits wooded country or stands of trees in open country, preferably near ponds and streams. Observations on roosting habits are few, and suggest that it probably roosts chiefly in trees, behind loose bark or in cavities [12], including woodpecker holes [15]. During migration it may be found in different habitats, including treeless prairie, and it may use a variety of roosts. For hibernation this species uses spaces under loose bark and hollow trees, rock crevices and sometimes buildings. It rarely enters caves, but may occasionally hibernate in silica mines in the United States [16]. The silver-haired bat is a hardy species, which has been captured flying at below-freezing temperatures (-2°C) [9]. It will hibernate north approximately to the -6.7°C mean daily minimum January isotherm [8].

Food

*Lasionycteris* feeds on a variety of insects including moths (Lepidoptera), Cercopids (Homoptera), Diptera, Hemiptera, Hymenoptera (primarily ants), Coleoptera and Neuroptera [3, 19, 20].

Activity and Behaviour

In Canada, *Lasionycteris* emerges early relative to sunset [1, 5], in contrast to the same species in more southern areas [11]. The earlier emergence is probably related to the shorter summer nights at higher latitudes. It is one of our slowest flying bats, which easily identifies it on the wing. Foraging takes place over small bodies of water in forested areas, sometimes close to the ground and at or below treetop level (7–15 m). The animal, flying erratically, with many twists and short glides, forages along the same circuit repeatedly.

Studies in Iowa and Montana found that feeding activity shows a major peak three hours after sunset with a lesser peak seven to eight hours after sunset [10, 11]. Barclay [1] found that this bat was active throughout the night in Manitoba from approximately 30 minutes after sunset to just before sunrise.

The silver-haired bat is solitary, or may occur in small groups of three or four individuals. A migratory species over most of its range it flies south between the middle of August and early October [1, 14, 17]. Winter records of this species in Canada are known only from southwestern British Columbia [4, 5, 18] and southern Ontario [17]. The return migration in spring probably takes place from about the middle of April to early summer. Barclay [1] reported the major influx near Delta, Manitoba, in late May and early June. Peterson [17] reported a specimen from York County, Ontario, taken in May. There is evidence to suggest that females migrate farther north than the males, resulting in a geographical segregation of the sexes during the summer [18]. This appears not to be the case in southwestern British Columbia where the population may not be migratory.

Little is known about reproduction in this species. It is assumed that breeding occurs during the fall migration. The timing of parturition in Canada is not known, but the presence of pregnant females with small embryos during the spring migration, the observation of a pregnant female with two embryos about 15 mm long in southern Quebec on 13 July, (NMC specimen), and a lactating female in Peace River, Alberta, on 22 July [18], suggest the first half of July as the period during which females give birth. A captive female was observed to give birth in a head-up position [12]. The young, numbering one or two, are hairless and pink with dark membranes at birth, and have closed eyes and folded ears. They are able to fly at three weeks of age, and mature sexually during their first summer.

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## Genus *Lasiurus* Gray, 1831
(f. Gk *lasios* hairy; *oura* tail)

Externally, *Lasiurus* is characterized by broad, bluntly rounded ears, short tragus, narrow wings, the presence of four mammae and an interfemoral membrane that is densely furred dorsally. The skull is very broad, deep and short. The extremely short and broad rostrum is quite distinct from that of any other native bat. There are 32 or 30 teeth. The dental formula is i1/3; c1/1; p1(2)/2, m3/3. The single upper incisor is in contact with the canine and the minute P3 is squeezed in between the canine and P4. *Lasiurus* is restricted to the New World, where it is found from Canada to southern South America, as well as on the Antilles, the Bahamas, the Galapagos and Hawaiian Islands. There are seven named species [1]; all roost in the foliage of trees and those in the temperate zones are migratory.

### References

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[2] Miller, G.S., Jr., 1897*a*

## *Lasiurus borealis* Müller
(f. L *boreas* north wind)

**Red Bat** — Chauve-souris rousse

1776 *Vespertilio borealis* Müller, Des Ritters Carl von Linné...vollständiges Natursystem..., Suppl. p. 20
1897 *Lasiurus borealis* Miller, N. Am. Fauna 13:105
Type locality: New York

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| N | 21 | 18 | 17 | 8 | 5 | 4 |
| $\bar{X}$ | 103.5 | 46.0 | 8.1 | 39.7 | 11.4 | 12.5 |
| SD | 8.24 | 6.55 | 0.87 | 1.96 | 0.59 | 3.34 |
| CV | 7.97 | 14.24 | 10.76 | 4.96 | 5.19 | 26.79 |
| OR | 87–120 | 36–65 | 7–10 | 36–42 | 10–12 | 10–17.4 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| N | 19 | 17 | 18 | 17 | 19 | 17 |
| $\bar{X}$ | 12.9 | 7.8 | 4.2 | 5.8 | 4.6 | 6.2 |
| SD | 0.45 | 0.25 | 0.18 | 0.21 | 0.23 | 0.34 |
| CV | 3.55 | 3.29 | 4.39 | 3.62 | 5.19 | 5.5 |
| OR | 12–13.6 | 7.2–8.2 | 3.9–4.8 | 5.4–6.2 | 4.2–5.0 | 5.6–6.8 |

### Description (Colour Plate III)

A medium-sized colourful bat. Wingspan 28–33 cm. Pelage full and soft, 17–18 mm long on the back. Colour varies, bright yellowish-red, orange or yellowish grey. Males usually more brightly coloured than females. Dorsal side of uropatagium densely furred, dense fur also extends onto the flight membrane to a line from the ankle to the middle of the humerus and continuing on the antebrachial membrane; small furred areas also present on either side of the proximal third of the fifth metacarpal and at the base of the thumb. Ventrally fur extends from the knee and along the forearm to the space between the third and fourth metacarpals and on the antebrachial membrane and the basal one-third of the uropatagium. Flight membranes blackish, but reddish brown to pinkish on and along forearm and along metacarpals. Ears short and rounded, pale coloured, inner side naked except for a few scattered hairs, basal two-thirds of outer side densely furred, the tip naked. Tragus short and broad. Feet small, less than half the length of the tibia, dorsal surface including toes covered with thick fur. Calcar short, with indistinct keel, extending less than halfway along the edge of the uropatagium, between foot and tip of tail. Metacarpals distinctly graduated, the third being the longest. Thumb well-developed, as in all our

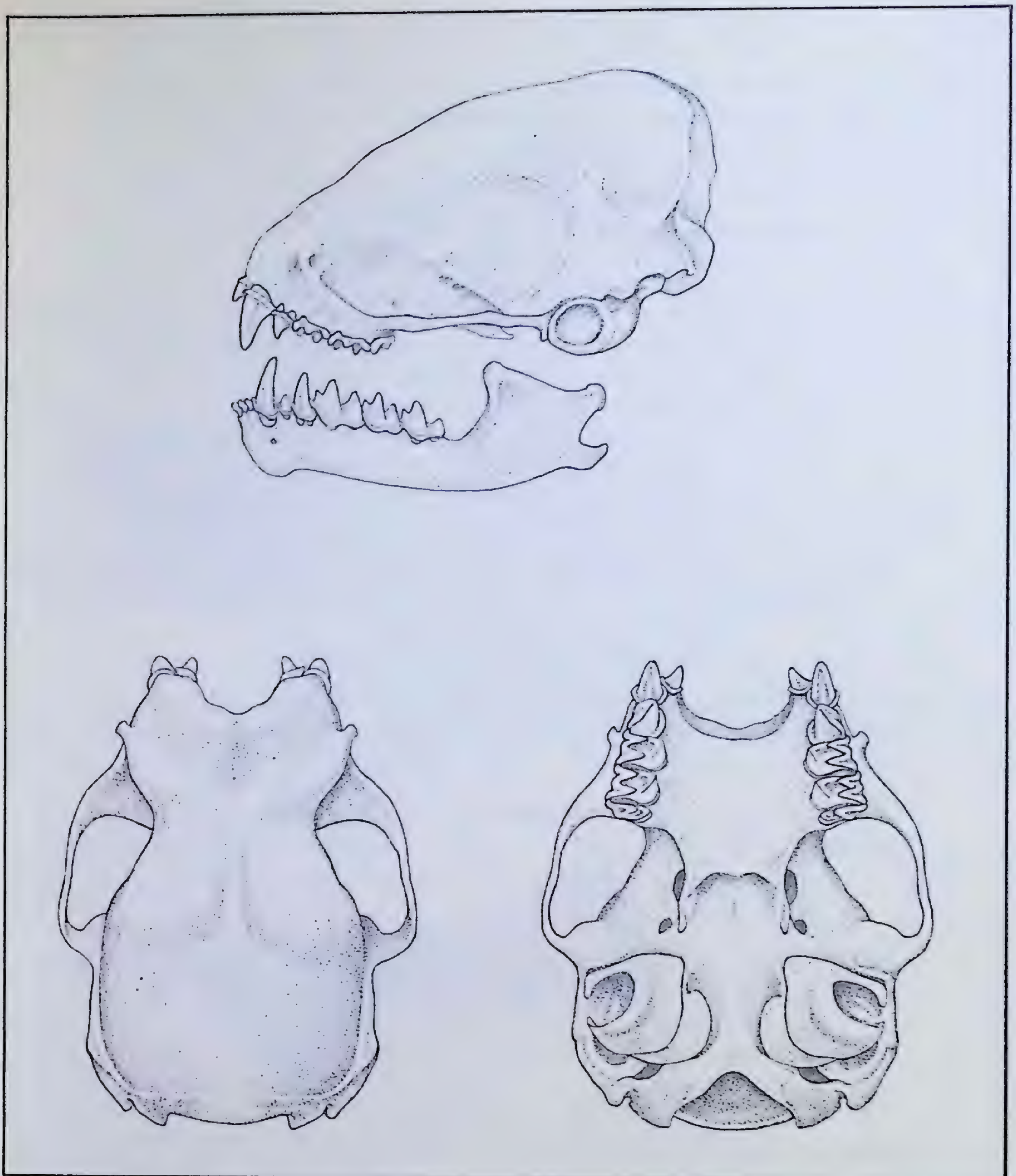

Figure 44. Skull of *Lasiurus borealis*

foliage roosting species, claw-bearing phalange conspicuously deep and laterally flattened. Skull broad and high, with very short rostrum and broad molars, dorsal profile nearly straight. Baculum with high proximal end and distal tip somewhat thicker and broader than shaft (Figure 31, Table 4). Chromosomes 2N = 28; FN = 46 [1].

Similar Species: This is one of our most distinct species, not easily confused with any other species. *L. cinereus* is somewhat similar to *L. borealis* but is much larger and grey with black-rimmed ears.


Distribution of *Lasiurus borealis*

## Distribution

The range of this species extends from the Maritimes to Saskatchewan with isolated and presumably accidental occurrences at points beyond. Because of the propensity of this strong flying migratory species to stray, its breeding range is difficult to delineate. In some presumably unsuitable areas of the country, red bats are present during migration, e.g. Barclay [3] found that they moved through the area near Delta, Manitoba, in spring and late summer, but were not present through the summer. Peripheral localities: *Alberta:* (1) Calgary. *British Columbia:* (2) mouth of Skagit River. *Manitoba:* (3) Wekusko. *New Brunswick:* (4) Saint-Léonard; (5) Saint John. *Northwest Territories:* (6) Coral Harbour, Southampton Island. *Nova Scotia:* (7) Sable Island. *Ontario:* (8) Favourable Lake; (9) North Point, 29 km N of Moosonee; (10) Bigwood; (11) Pancake Bay; (12) Silver Islet. *Quebec:* (13) Pointe-Fortune; (14) Québec. *Saskatchewan:* (15) Reindeer Lake; (16) 19 km SE of Prince Albert; (17) Saskatoon; (18) Expanse.

South of the international border, the species is found west to California and south to southern South America (Chile, Argentina). In North America, it appears to be most abundant in the midwestern United States in summer, wintering mostly in the southern states.

## Systematics

Three subspecies are recognized in the North American part of the species' range, of which two have been recorded in Canada. *L. b. borealis* Müller is the most widespread form in Canada.

*L. b. teliotis* (H. Allen) 1891, Proc. Am. Philos. Soc. 29:5.
A slightly smaller, more brightly coloured western form, only known from one specimen in Canada, which was collected near Skagit, British Columbia.

## Biology

The red bat is found near forests or in more open cultivated areas where shade trees are present. It roosts almost exclusively in the foliage of trees [2, 5, 7]. Sites from 1 to 6 m above the ground, in dense foliage, are usually selected for roosting. As a rule these roosting sites provide cover all around but are open below, allowing the animal simply to drop down to begin its nightly forays [7]. Although it will occasionally enter caves in late summer [2, 28], the red bat does not hibernate there, but migrates to areas with milder climates, generally south of latitude 40°N [6]. Here it hibernates in the foliage of trees, in hollow trees, woodpecker holes [10] or under bark. Torpor may be interrupted frequently depending on the weather. Unlike bats hibernating in caves, this species responds to subfreezing temperatures by increasing its metabolism just enough to keep its body temperature above the critical lower limit of -5°C [30]. The insulation provided by the long dense fur keeps heat loss to a minimum [33]. Habitat

The red bat feeds on a wide variety of insects including both hard-bodied Coleoptera and soft-bodied Lepidoptera as well as Homoptera and Orthoptera (crickets) [31, 34]. The red bat itself will sometimes fall prey to other animals [8, 9, 15, 22]. It is possible that this species is more vulnerable to predation by birds such as jays (*Cyanocitta cristata* and probably other species as well) [9, 15] because of its roosting habits or by hawks (*Accipiter* spp.) [8] during migration when flight activity may continue until 1.5 hours after daybreak. The larger litter size of this species may be a response to these increased risks to predation.

In summer the red bat emerges half an hour after sunset in southern Canada (Delta, Manitoba) [3]. At more southern latitudes, in the United States, it usually starts foraging one to two hours after sunset [16, 17]. In their winter quarters, many of these bats may arouse from torpor and feed in the late afternoon, on warm winter days, when the temperature is around 19°C [2, 19]. A few have been observed to be active at temperatures down to 7°C [19]. In summer the feeding activity is reported to show a peak around two to three hours after sunset and a secondary lesser peak around five to six hours after sunset in Iowa [18]. These bats have been reported to fly high, near or above treetop level, foraging over streams and forest during the early part of the evening flight [2]. During this phase their flight is said to be slow and erratic. Later on, they descend and hunt at heights between the treetops and the ground. Their flight is then fast and direct, while they hunt regularly over the same ground.

In its daytime roost this bat usually hangs from the petioles of leafs or occasionally from twigs. Its resemblance to a dead leaf while thus suspended makes the animal difficult to detect. While roosting, the red bat is usually solitary or found in family groups of up to five individuals. When foraging, however, it may be found hunting in groups of 20 to 30 [19].

Fall migration begins in late August and September and continues into October. The latest records for Ontario are 14 October (Ottawa) and 27 October (Middlesex County). In Delta, Manitoba, red bats pass through from the latter half of July to the end of September [3]. Most oceanic records reported are from the period of late August and September [12, 21, 24, 27]. Most of the spring migrants arrive in Canada in May, although there is one record as early as 11 March.

Mating takes place in August and September [11, 14], when males can be seen pursuing females. Copulation may be initiated in the air [37]. Fertilization occurs in spring. The gestation period of 80 to 90 days [16] culminates in the birth of one to four, rarely five, young in June. The average number of young is 2.3 [34]. At birth the young weigh approximately 0.50 g, are hairless and have closed eyes [29]. They are thought to be capable of flight between three and four weeks of age, and weaned between five and six weeks [2]. When away from the mother, the young make clicking noises, which elicit a positive response in her. Except perhaps when they are very young, the offspring are left at the roost when the female goes out hunting. Occasionally females have been found with young attached [35], whose weight

caused them to fall to the ground and to remain grounded. These females were presumably attempting to transfer their young to a different roost, or since many of the grounded red bats have been found after storms, it is likely that these were blown from their roosts.

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## *Lasiurus cinereus* (Palisot de Beauvois)
(f. L *cinereus* ashen)

**Hoary Bat** — Chauve-souris cendrée

1796 *Vespertilio cinereus* (mispelled *linereus*) Palisot de Beauvois, Catalogue raisonné du muséum de Mr. C.W. Peale, Philadelphia, p. 18
1864 *Lasiurus cinereus* H. Allen, Monogr. Bats N. Am., Smithson. Misc. Collect. 7 (publ. 165):21
Type locality: Philadelphia, Pennsylvania

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| N | 9 | 9 | 10 | 6 | 6 | 5 |
| $\bar{X}$ | 126.9 | 55.1 | 10.8 | 56.0 | 14.0 | 27.6 |
| SD | 12.84 | 8.44 | 1.22 | 1.48 | 1.26 | 1.98 |
| CV | 10.12 | 15.33 | 11.38 | 2.67 | 9.04 | 7.19 |
| OR | 99–140 | 40–64 | 9–12 | 54–58 | 13–16 | 25.4–30.3 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| N | 11 | 11 | 11 | 11 | 11 | 11 |
| $\bar{X}$ | 16.6 | 10.2 | 5.3 | 7.0 | 6.2 | 8.6 |
| SD | 0.35 | 0.25 | 0.24 | 0.13 | 0.28 | 0.35 |
| CV | 2.14 | 2.55 | 4.67 | 1.98 | 4.57 | 4.07 |
| OR | 16.2–17.2 | 9.8–10.6 | 4.7–5.6 | 6.7–7.2 | 5.8–6.6 | 8.2–9.3 |

### Description (Colour Plate III)

Size large; aside from size and colour, similar to *L. borealis*; wingspan 34–41 cm. Colour of pelage, a mixture of light yellowish-brown, dark brown and white; fur on dorsum, when parted, showing four bands of colour, from base up blackish-brown, yellowish-brown, blackish-brown band and terminal band of silvery-white tips; tufts of fur at base of thumb and wing membrane cream coloured; fur distributed as in *L. borealis*. Flight membranes blackish-brown except for brown strips along forearm and metacarpals. Ear short, rounded, with dark-brown or blackish margin and basal half of outer side densely furred; tragus short, similar to that of *L. borealis*. Foot relatively small, approximately half as long as tibia, dorsal side densely furred. Calcar approximately twice as long as foot, with narrow keel. Wings long and narrow, metacarpals graduated, with third and fourth metacarpal longer than forearm. Thumb well developed, length approximately 20% of forearm length, similar in form to that of *L. borealis*.

Skull short, broad and high, as in *L. borealis* but larger, teeth robust. Baculum approximately 1 mm long, stout, rounded shaft with swollen cylindrical base, distal portion with upturned terminal tips (Figure 31, Table 4). Chromosomes 2N = 28; FN = 46 [2].

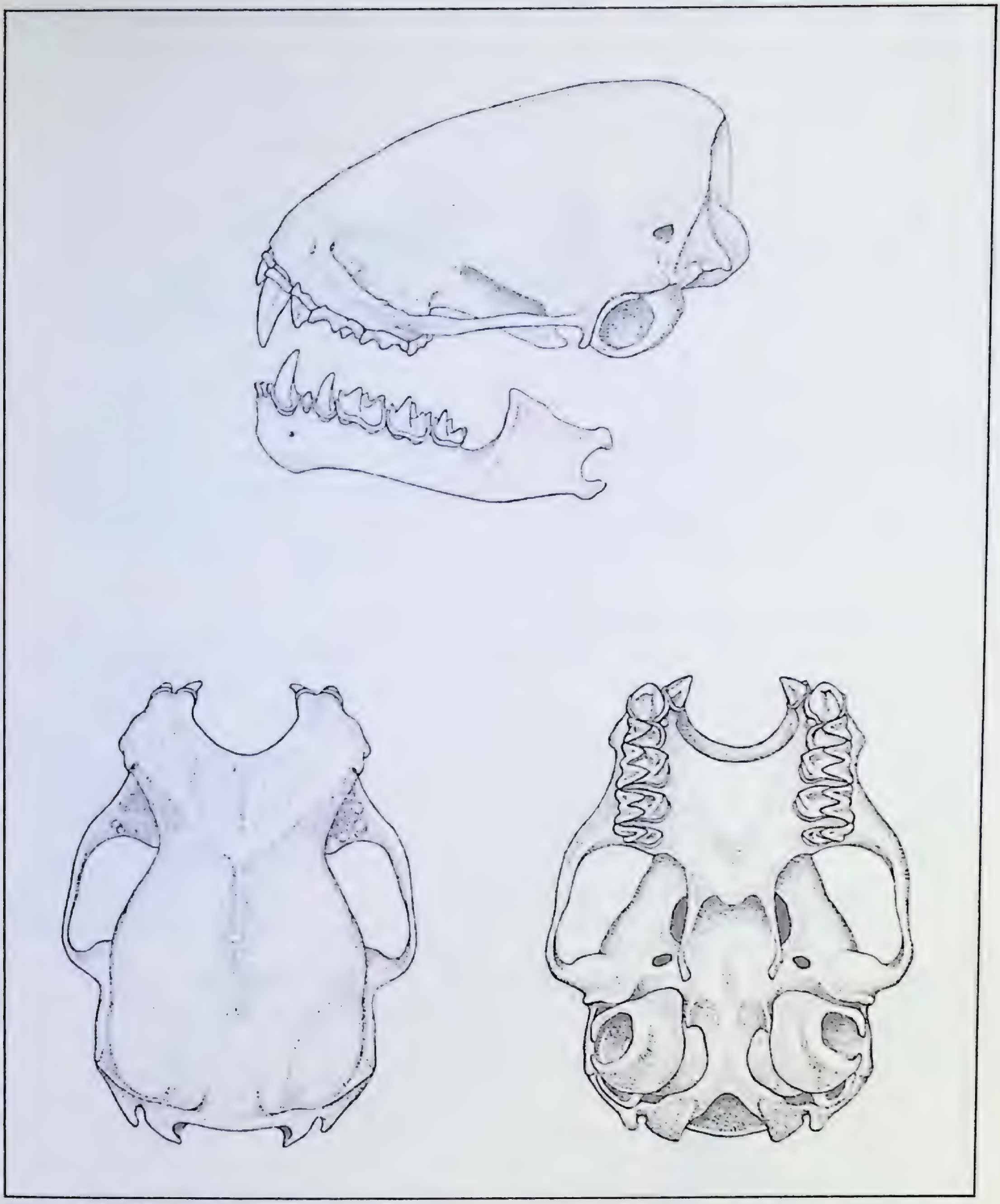

Figure 45. Skull of *Lasiurus cinereus*

Similar Species: This distinctive bat is easily identified. The superficially similar *Lasionycteris noctivagans* can be readily distinguished by its much smaller size and lack of fur on feet, ears and ventral surface of wing membranes.

**Distribution**

The hoary bat is widely distributed in Canada, and although it is rarely seen, biologists using bat detectors have found that it is very common in many places. Individuals of this species have been recorded from widely scattered localities far beyond areas that are considered to offer suitable habitat. As is the case with *L. borealis*, delineation of the northern limits of the breeding range is difficult. Females appear to outnumber males in the northern part of the range in summer. Peripheral localities: *Alberta*: (1) Grimshaw; (2) Athabasca River at La Biche River; (3) Beaverlodge. *British Columbia*: (4) Alta Lake; (5) Victoria. *Manitoba*: (6) Amaranth. *New Brunswick*: (7) Fredericton. *Northwest Territories*: (8) Bear Island; (9) Fort Resolution. *Nova Scotia*: (10) Halifax; (11) Seal Island. *Ontario*: (12) North Point, 29 km N of Moosonee; (13) Thunder Bay (Port Arthur); (14) Malachi.


Distribution of *Lasiurus cinereus*

*Quebec*: (15) Hull. *Saskatchewan*: (16) Emma Lake. *L. cinereus* has the most extensive range of any New World vespertilionid, extending from Canada south to Chile, Argentina and Uruguay. It is the only bat found on the Hawaiian Islands and wanderers have also been reported from such widely scattered localities as Iceland, the Orkneys and Bermuda.

## Systematics

*L. cinereus* displays little geographic variation on the North American continent. The resident population in the Hawaiian archipelago is considered subspecifically distinct (*L. c. semotus*).

## Biology

Habitat

The hoary bat is a tree bat that roosts in foliage, usually near the end of branches, 3 to 12 m above the ground, usually on the edge of clearings or fields [4, 9]. It has also been found in orchards and there is a report of one having been found in a woodpecker hole in a dead tree [10]. It enters caves only very rarely in late summer. Because of its superb cryptic coloration, which blends in particularly well with the lichen-encrusted branches of northern forests, this bat is rarely seen on its roost.

Food

The hoary bat feeds chiefly on large moths and to a lesser extent on other insects including Coleoptera, Hymenoptera and Odonata [6, 7, 18, 22, 23]. A few observations of hoary bats attacking or preying on smaller bats may not represent the behaviour of normal bats but that of rabid animals [5].

Activity and Behaviour

In most of the United States this species emerges late usually when it is dark [20], except during migration and on warm days in the wintering areas. In Iowa feeding activity peaks between four to five hours after sunset and continues through the night at decreasing levels with a minor secondary activity peak several hours before sunrise, coinciding with increased insect activity [12]. At Delta, Manitoba, Barclay [4] reported that hoary bats were active from 30 minutes after sunset until just before sunrise. The shortness of northern nights is probably responsible for the early emergence. The hoary bat is an open air forager whose flight is fast, direct and usually high (7–15 m) [4]. Its size and characteristic flight pattern readily identify it in flight, when there is sufficient light to see it. Barclay [4] observed that individual *L. cinereus* established feeding territories from which they chased other bats.

In the breeding range this bat is usually solitary or found in family groups consisting of a female and her young [4, 19]. Concentrations of these bats may form during migration. Spring migration probably occurs during May and early June, with the females migrating earlier that the males. The earliest collection date of specimens from Canada that have been examined was 9 June. There appears to be a degree of geographical segregation of the sexes during the summer [11], with the females predominating in the north and east and the males in the west. However, at Delta, Manitoba, Barclay [4] caught equal numbers of adult

males and females in summer. Further substantiation of the reported seasonal geographic segregration of the sexes appears necessary.

The fall migration takes place from mid-August to October. At Delta, peak activity was observed in the first half of September [4]. Peterson [17] mentions an observation in York County, Ontario, on 23 October and there is one specimen in the National Museum of Natural Sciences that was collected in October in Victoria, B.C. The majority of hoary bats are thought to winter in the southern United States and Mexico, there being few records north of New Mexico in the west and Georgia and South Carolina in the east between November and February [11]. Sporadic winter records for several northern states (Michigan, New York, Connecticut, Indiana) indicate that some individuals may winter farther north [3, 21].

**Reproduction and Ontogeny**

There is no information on mating in hoary bats, which may take place before migration or at the wintering grounds. By the time the females fly north in spring they are pregnant and births occur between late May and early July. Reported dates for Canada fall within a period from mid to late June [4, 14, 16]. Litter size is almost always two, but single births occur [3, 4, 19]. Observation of a small number of captive bats suggests that females of this species give birth in a horizontal position suspended from thumbs and feet with the uropatagium curled over the vaginal opening [8]. The young, which are delivered by breech presentation, grasp the mother with thumbs and feet while still connected to her by the umbilical cord, which serves as a safety line. The explusion of the placenta takes place sometime after the birth (in one case 90 minutes after) and the placenta is usually eaten by the mother severing the connection with the umbilical cord.

The newborn young are covered with fine silver-grey hair on the back of the head, shoulders, uropatagium and feet but naked elsewhere. The forearm length measures from 16–20 mm. The rims of the ears and the fingers, as well as the furred parts, are darkly pigmented. The ears and eyes are closed and open in three and twelve days respectively [8, 15]. The female may carry the young in flight until they are about a week old [8]. By day 22 the young resemble the parent in pelage colour and by day 33 they are weaned and capable of sustained flight [8]. Barclay [4] observed that family groups appear to stay together for a relatively long time (over two weeks) after the young are volant.

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## Genus *Plecotus* Geoffroy, 1818

(f. Gk *plekō* I twine, I twist; *ous*, genit. *ōtos* ear)

*Plecotus* is characterized by extremely large ears, joined at the base across the forehead and well-developed glandular swellings between the eye and the nostril, which are particularly conspicuous in the subgenus *Corynorhinus*. The skull is narrow and highly arched. There are 36 teeth. Dental formula i2/3; c1/1; p2/3; m3/3. All species of the genus that have thus far been investigated possess a similar karyotype, $2N = 32$; $FN = 50$. *Plecotus* is a Holarctic genus with two Palearctic species (subgenus *Plecotus*) and three Nearctic species (subgenus *Corynorhinus*). *Idionycteris, Euderma* and *Barbastella* are related genera [2]. The genus *Idionycteris* is sometimes considered a subgenus of *Plecotus*, but its morphology and karyotype show it to be more divergent from *Plecotus* and more closely related to *Euderma*.

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## *Plecotus townsendii* Cooper
(named after J. Townsend)

| **Western Big-eared Bat** (Townsend's Big Eared Bat) | **Oreillard de Townsend** |
|---|---|

1837 *Plecotus townsendii* Cooper, Ann. Lyc. Nat. Hist. New York 4:73
1897 *Corynorhinus macrotis townsendii* Miller, N. Am. Fauna 13:53
1955 *Corynorhinus townsendii townsendii* Handley, J. Wash. Acad. Sci. 45:147
1959 *Plecotus townsendii* Handley, Proc. U.S. Nat. Mus. 110:95–246
Type locality: Columbia River, Oregon

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 14 | 14 | 14 | 12 | 10 | 1 |
| **X̄** | 101.5 | 44.8 | 11.1 | 42.6 | 35.8 | 6.9(♂) 10.6(♀) |
| **SD** | 5.63 | 7.03 | 0.61 | 1.02 | 2.04 | – |
| **CV** | 5.56 | 15.69 | 5.56 | 2.41 | 5.71 | – |
| **OR** | 88–110 | 32–62 | 10–12 | 41–46 | 33–39 | – |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 11 | 10 | 12 | 11 | 12 | 11 |
| **X̄** | 16.2 | 9.2 | 3.6 | 5.7 | 5.3 | 6.1 |
| **SD** | 0.28 | 0.17 | 0.08 | 0.16 | 0.15 | 0.08 |
| **CV** | 1.73 | 1.85 | 2.50 | 2.98 | 2.93 | 1.36 |
| **OR** | 15.8–16.8 | 8.8–9.4 | 3.4–3.7 | 5.4–6.0 | 5.1–5.6 | 5.9–6.2 |

### Description (Colour Plate IV)

A medium-sized bat with very large ears (80% more of forearm length) and two prominent glandular masses on dorso-lateral surface of snout; wingspan 29–31 cm. Fur uniform pale grey-brown to dark brown on back, a little lighter below; hairs grey at base, pale brown or darker brown on top. Flight membranes and ears brown. Ears very long, tragus approximately one-third as long. Foot approximately half as long as tibia; calcar without keel and extending approximately halfway down edge of uropatagium. Wings relatively broad; metacarpals subequal. Skull highly arched, outer upper incisor unicuspid. Baculum saddle-shaped (Figure 31, Table 4).

Similar Species: *Antrozous pallidus*: larger with broader ears, light-yellowish fur pale at base, no lumps on snout. *Plecotus rafinesquii* (the eastern big-eared bat, eastern United States, not recorded from Canada): whitish underparts, grey dorsal fur, long hair on toes and bicuspid upper incisors.

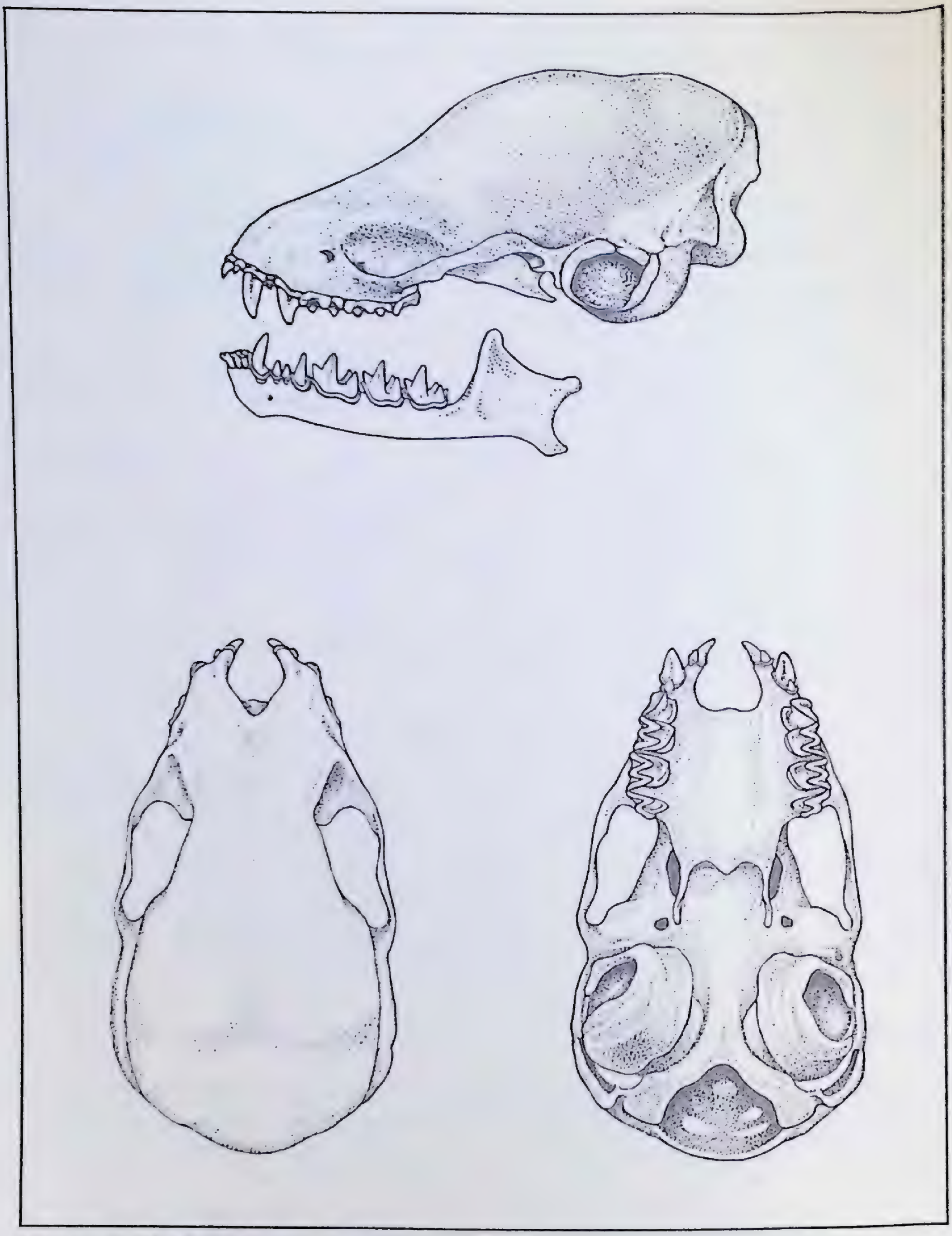

Figure 46. Skull of *Plecotus townsendii*

## Distribution

In Canada, this species is found only in British Columbia, where it is nowhere abundant. Peripheral localities: *British Columbia*: (1) Williams Lake; (2) Adams River; (3) Kootenay River, near Creston; (4) Victoria; (5) Fishermans Cove; (6) Comox.

This bat is also found in the western United States and in parts of Mexico. Isolated relic populations occur in Kansas, Oklahoma, Texas, Missouri, Arkansas, Kentucky, Virginia, and West Virginia [8].


Distribution of *Plecotus townsendii*

## Systematics

Two subspecies occur in Canada.

*P. t. townsendii* Cooper, 1837, Ann. Lyc. Nat. Hist. New York 4:37.
A dark-coloured form. Distribution: Coastal southern British Columbia, including Vancouver Island.

*P. t. pallescens* Miller, 1897, N. Am. Fauna 13:52.
A paler desert form. Distribution: Interior British Columbia.

For information on relationships of *P. townsendii* to other species, see account of genus.

## Biology

The habitat of this species includes humid coastal forest as well as arid scrub and pine forest. Caves, abandoned mines and buildings are used for roosting. Caves and old mines within the summer range serve as hibernacula. Habitat

Nothing is known about the feeding habits of this bat in Canada, but studies in the United States have shown it to feed chiefly on small moths [11, 13]. Smaller quantities of other insects including Coleoptera, Diptera, Hymenoptera and Neuroptera are also consumed. Food

There is no information on population structure and dynamics. The greatest longevity recorded for this species is 16.4 years [9]. Population

The western big-eared bat begins its hunting flight after darkness has fallen and is therefore rarely seen. This species appears to be predominantly an aerial forager, capturing its prey in flight near or among vegetation. There are no observations in the literature of this species gleaning prey off foliage. There are probably two peaks in feeding activity, one shortly after emergence and another one toward dawn [8]. Between feeding periods it uses night roosts [10] and does not return to the day roost until just before dawn. It is a manoeuvrable and swift flier, capable of a variety of flight patterns [1]. It may dart swiftly, hover, or fly slowly, alternating deep wingbeats with short glides. While hovering or flying slowly, the ears are held in a vertical position and are then easily seen. At other times they are held horizontally. At rest or during hibernation the ears may be coiled back, while the tragus remains erect. This bat produces an FM call of a relatively low intensity and frequency, which would make it more difficult to be detected by the tympanate moths it preys on. *Plecotus* differs from other native bats in that the echolocation sound may be emitted through the mouth or through the nostrils [4]. This bat usually hangs free from the ceiling or along the wall, never entering cracks or crevices. Activity and Behaviour

In summer the females form maternity colonies of a dozen to over 100 individuals, while the males lead solitary lives [1, 7, 10]. During hibernation they may be suspended singly or in small clusters of up to 50 individuals in relatively exposed situations [7]. There is no evidence that this species performs long

distance flights to reach its hibernacula [1, 7, 10], but instead uses suitable sites within its summer range.

Reproduction and Ontogeny

Reproduction has not yet been studied in Canada. A study in California found that mating occurs from October to February, followed by ovulation and fertilization between February and April [7]. After a variable gestation from 56 to 100 days, depending on the temperature of the surroundings, a single young is born in late May or early June. Parturition occurs in mid-July in British Columbia [2] and the first half of July in Washington [12]. The young are born naked and with closed eyes, although the ears are large. They weigh about 2.4 g at birth and have a forearm length of 16.1 mm. Within four days a short grey cover of hair appears and after seven days the ears assume the erect position of the adults. The eyes open shortly after. They are able to vocalize within a few hours, which allows the mother to seek out her own young from a cluster of many. The young are able to fly when they are about three weeks old and at one month they are almost full grown. The maternity colonies begin to disband in August and September in California [10]. Females attain sexual maturity at approximately four months. Males do not mate in their first year.

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## Genus *Euderma* H. Allen, 1892
(f. Gk *eu* good, nice; *derma* skin)

Externally this genus is characterized by large ears joined together basally across the forehead, a tragus without basal lobe but united with the basal lobe of the auricle, the lack of glandular masses on the snout and the striking black-and-white colour pattern of the pelage.

The skull is similar to that of *Plecotus* but has an exceptionally elongated braincase, a bifid median postpalatal process, and auditory bullae with approximately elliptical outline. There are 34 teeth. Dental formula i2/3, c1/1; p2/2; m3/3. P1 is minute, the lower canine small, no higher than p4 and with its anterolingual secondary cusp nearly equal in height to the primary cusp, and p4 possesses a well-defined metaconid cusp.

*Euderma* is a monotypic genus restricted to western North America.

### References

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## *Euderma maculatum* (J.A. Allen)
(f. L *macula* spot)

**Spotted Bat** — **Oreillard maculé**

1891 *Histiotus maculatus* J.A. Allen, Bull. Am. Mus. Nat. Hist. 3:195
1894 *Euderma maculata* H. Allen, Bull. U.S. Nat. Mus. 43:61
1897 *Euderma maculatum* Miller, N. Am. Fauna 13:46
Type locality: Near Piru, Ventura Co., California

External Measurements

| | TL | T | HF | FA | E |
|---|---|---|---|---|---|
| Females* | | | | | |
| **N** | 3 | 3 | 4 | 4 | 2 |
| **X̄** | 111 | 49 | 11 | 50 | 42 |
| **OR** | 107–115 | 47–50 | 10–12 | 48–51 | 37–47 |
| Males* | | | | | |
| **N** | 5 | 5 | 2 | 6 | 5 |
| **X̄** | 110 | 47 | 10 | 49 | 41 |
| **OR** | 107–114 | 46–48 | 9–10 | 48–50 | 39–43 |
| | Adult Female from British Columbia (BCPM 10799) | | | | |
| | 125 | 55 | 10 | 54 | 39 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| Females* | | | | | | |
| **N** | 2 | – | 2 | 1 | 1 | 2 |
| **X̄** | 18.9 | – | 4.3 | 5.7 | 6.0 | 6.8 |
| **OR** | 18.8–19.0 | – | 4.2–4.3 | - | - | 6.7–7.0 |
| Males* | | | | | | |
| **N** | 2 | – | 2 | 2 | 2 | 2 |
| **X̄** | 18.7 | – | 4.0 | 4.7 | 6.0 | 6.5 |
| **OR** | 18.4–18.9 | – | 3.9–4.0 | 5.5–5.9 | 5.8–6.1 | 6.4–6.5 |
| | Adult Female from British Columbia (BCPM 10799) | | | | | |
| | 19.4 | 10.7 | 4.1 | 6.0 | 6.2 | 7.3 |

*Measurements from Handley 1959. MTL taken parallel to long axis of tooth row by him, and parallel to long axis of skull by me.

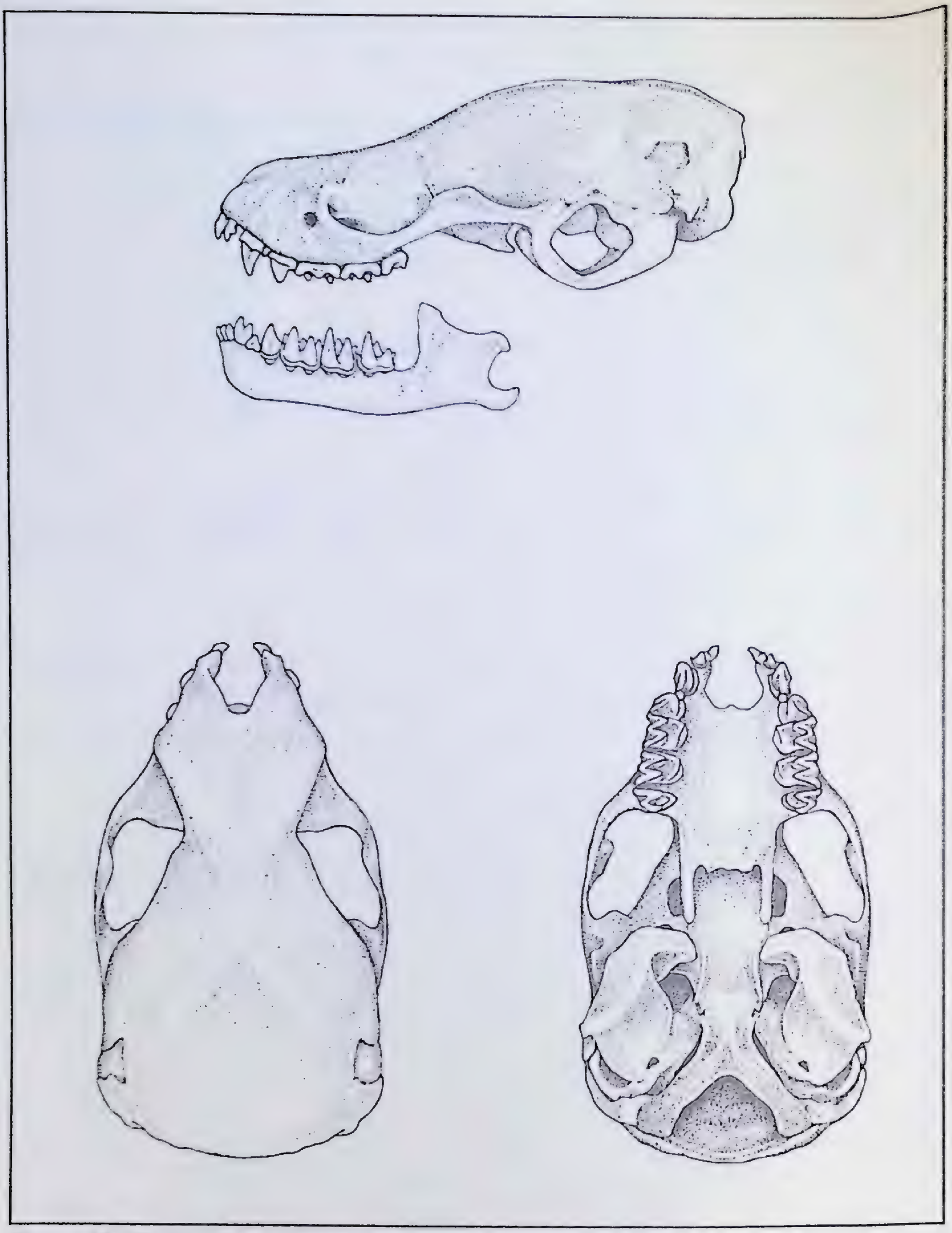
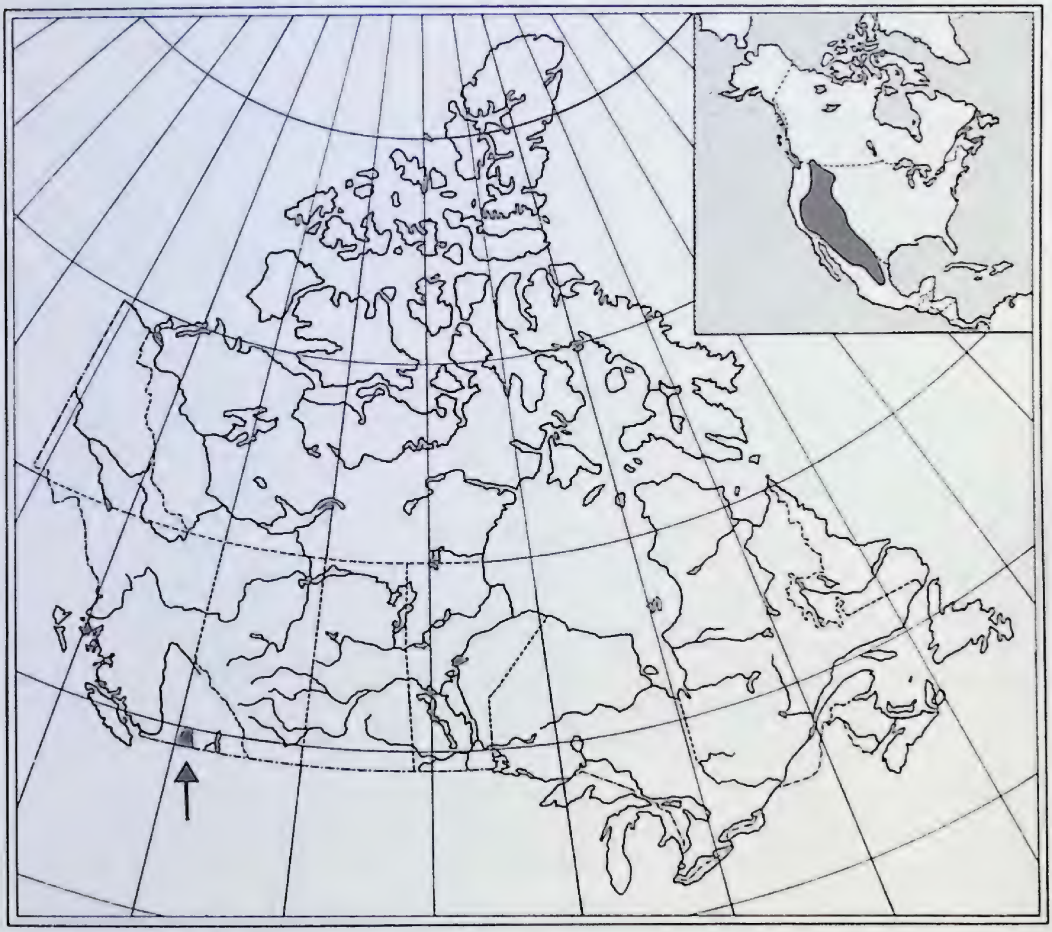


Figure 47. Skull of *Euderma maculatum*

## Description (Colour Plate IV)

A large, spectacularly coloured bat with a wingspan of around 35 cm. Fur black on dorsum with three large round white spots (approximately 15 mm in diameter), one on each shoulder and one on rump, smaller white patches at the posterior base of each ear; venter white; basal fur black throughout except for white areas at base of ears; circular, naked, non-glandular area on throat. Ears enormous, pinkish-grey in colour with transverse ribs extending to posterior border of auricle. Membranes thin, pliable, pinkish-red to grey-brown in live animal; last caudal vertebra is free of the uropatagium. Calcar not keeled. For skull characters and further details see description under genus. Second phalanx longer than first phalanx in third finger. Other parts of the postcranial skeleton have been partly described by Hall [9] but morphology of the baculum is still unknown.

Similar Species: *Euderma* cannot be confused with any other bat.



Distribution of *Euderma maculatum*

## Distribution

In Canada the spotted bat is known only from the southern Okanagan Valley, where its presence was first detected in 1979. The following year the identity of the species was confirmed by the collection of one female specimen, deposited in the British Columbia Provincial Museum, Victoria [20]. Field observations and a number of live captures further confirmed that a resident breeding population of this species is present. The species has now been observed at many localities within a relatively confined area [12]. Peripheral localities: *British Columbia*: (1) Skaha Lake, east shore 4.2 km S of the north end of the lake; 3.5 km E of Vaseux Lake; 4 km W of Tugulnuit; and 1 km SW of Twin Lakes, Similkameen District.

The centre of the species' North American distribution appears to be in the southwestern United States, where it has been most frequently reported from California, Arizona, New Mexico, southern Colorado and southern Utah. The species has also been reported in Idaho, Montana, Oregon, Nevada and Texas and in Mexico south to the state of Queretaro [18].

## Systematics

Because of the scarcity of specimens in collections no analysis of geographic variation in this species has been done and no subspecies are recognized. *Euderma, Idionycteris, Plecotus* and *Barbastella* are thought to have evolved from a common myotine stock. The karyotype of *Euderma* (2N = 30, FN = 52, autosome pairs 11 SM; 1 ST; 2 A: X is SM; Y is A) is most similar to that of *Idionycteris phyllotis*, its nearest living relative [17, 20].

## Biology

Habitat

*Euderma* is possibly one of the rarest North American bats. It has been recorded from a wide range of habitats in the western mountain regions of the continent, most often in rough, rocky, semi-arid and arid terrain, varying from ponderosa pine (*Pinus ponderosa*) forest, to scrub country and open desert [18].

In British Columbia the habitat where spotted bats hunt consists of open ponderosa pine forest up to elevations between 700 and 800 m, and observations suggest that their day roosts are situated in high cliffs [12, 14, 21]. These bats crawl with ease both on horizontal and vertical surfaces, which facilitates their movement in rock crevices where they roost [3, 12]. Information on the habits of this species in winter are thus far entirely lacking.

Food

The food habits of the spotted bat in Canada are not known, but three studies in the southwestern United States all showed an overwhelming preponderance of moths in the diet [7, 15, 16].

Activity and Behaviour

Observations done during field studies in the Okanagan Valley [12, 21] indicate that the spotted bat emerges at dusk when it is quite dark (approximately 49 minutes after sunset) and returns to its day roost at dawn (approximately 67 minutes before sunrise). The relatively low aspect ratio and low wing loading suggest that this bat has a relatively slow, manoeuvrable flight. As flight speed is also positively correlated with forearm length (i.e. size) [10], *Euderma*'s flight in the field would appear faster than that of

smaller species with similar aerodynamic characteristics. It flies high, usually between 10–15 m, at or above treetop height [12, 21]. During these studies this bat was never observed to fly in or close to vegetation or to land on the ground to capture prey in the manner of *Antrozous pallidus*. It captures its prey flying.

One study suggests that the spotted bat may use a foraging strategy that involves hunting a regular beat and searching the clearings in the pine forest along it for prey [20]. The bats displayed a remarkable punctuality in making their rounds, arriving at various points along their route at the same time every night. In spring the bats spent 3 to 5 minutes per clearing, but later during the summer more time was spent around the same area, where they retraced definite circuits flying at or above treetop height. It seems likely that change in the pattern of foraging is related to increased prey availability in the later season. Another study [12] observed a predictable pattern of foraging from spring (May) to midsummer (July) consisting of relatively long foraging sessions, and a less predictable pattern later in summer consisting of shorter foraging periods at each site. The apparent contradiction in the results of the two studies probably reflects the variability of the bat's behaviour in response to changes in one or more factors in the environment (e.g. abundance and distribution of prey species).

Individuals using adjacent hunting grounds showed evidence of mutual avoidance, which can be interpreted as a spacing mechanism reducing intraspecific competition. The bats, always hunting alone, were observed to turn away when encountering one another near the boundary of their hunting ranges. If the neighbour was absent, no such behaviour was observed; on the contrary, the bat would unhesitatingly fly into the space it had previously avoided. Echolocation calls, by communicating an individual's presence, appear to be the principal means used by these bats to space themselves in suitable foraging habitat [12, 13].

It may be that the conspicuous colour pattern of this species also has a signal function that may play a role in mutual avoidance on the hunting range. An earlier suggestion that the adaptive function of the unusual colour pattern might be a cryptic one [2], making the bat less noticeable as it roosted on exposed rock surfaces, seems unlikely now that there is increasing evidence that this species roosts in crevices hidden from potential predators. It is conceivable that at close range the colour pattern acts as a visual signal, either alone or together with acoustic signals, communicating presence to conspecifics. It seems less likely that it would function as an aposematic coloration directed at other species.

The spotted bat has a loud high-pitched echolocation call that is clearly audible to the human observer at distances of 250 m or more [12, 13, 21]. The call consists of a double or single steep frequency modulated pulse with a fundamental frequency sweeping from 12–6 kHz. The call is repeated at a rate of 2–6 per second. The intensity of the call is moderate (estimated sound pressure level of 80–90 dB at 10 cm, compared to 110 dB at 10

cm for *M. lucifugus* [21]. The medium intensity, low-frequency echolocation call may represent an adaptation for hunting of large tympanate moths at long range and it may enhance the effectiveness of the call as an intraspecific territorial advertisement [13]. The low frequency allows for long-range detection of the prey, as well as increased range of audibility by other bats, because of the reduced attenuation and resulting good propagation qualities of low-frequency sound. In addition the relatively low intensity of the sound, which the moth cannot detect at long range, allows the bat to approach the moth more closely and enhances the chance of a successful pursuit.

Reproduction and Ontogeny

Very little is known about reproduction of this species. The time at which copulation occurs is not known. In the southern part of its range parturition probably occurs before mid-June. The female collected in British Columbia on 16 June was pregnant and contained an embryo (crown-rump length 29 mm), suggesting that the time of birth is somewhat later in the north. Evidence points to production of a single young [8, 17], which is born in an altricial condition, lacking any suggestion of the adult colour pattern and weighing about 4 g [1, 4, 6, 17].

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## Genus *Eptesicus* Rafinesque, 1820

(f. Gk *eptēn*, aorist of *petomai*
to fly; *oikos* house)

This genus is characterized by the reduction in the number of premolars, giving it a total of 32 teeth. Dental formula i2/3, c1/1, p1/2, m3/3. The skull is heavily built and has a broad rostrum relative to the braincase. The latter has a nearly straight dorsal profile, rising gradually from the top of the nasals to the occiput. The ears are relatively short, broader than long and the tragus is short and rather blunt. The species in the genus vary considerably in size (FA 38–55 mm). The genus is cosmopolitan, with approximately 33 species. There are seven species in the Americas, ranging from Canada to Argentina and Uruguay. *Eptesicus* is morphologically similar to the Palearctic genus *Vespertilio* and has morphological and karyological similarities to certain species groups of *Pipistrellus*, which should perhaps be placed in *Eptesicus* [2]. Chromosomal banding patterns suggest that *Eptesicus* is related to *Nycticeius, Rhogeessa* and *Antrozous* [1].

### References

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## *Eptesicus fuscus* (Palisot de Beauvois)
(f. L *fuscus* dusky)

**Big Brown Bat** — **Sérotine brune**

1796 *Vespertilio fuscus* Palisot de Beauvois, Catalogue raisonné du muséum de Mr. C.W. Peale, Philadelphia, p. 18
1900 *Eptesicus fuscus* Méhely, Magyarorszag denevéreinek monographiaja (Monographia Chiropterorum Hungariae), p. 206
Type locality: Philadelphia, Pennsylvania

External Measurements and Weight

| | TL | T | HF | FA | E | W |
|---|---|---|---|---|---|---|
| **N** | 117 | 118 | 115 | 37 | 38 | 28 |
| **$\bar{X}$** | 115.3 | 44.5 | 11.7 | 47.4 | 16.1 | 17.9 |
| **SD** | 7.54 | 5.28 | 1.38 | 2.46 | 1.89 | 3.24 |
| **CV** | 6.54 | 11.87 | 11.83 | 5.2 | 11.75 | 18.1 |
| **OR** | 93–130 | 23–59 | 9–15 | 41–52 | 12–19 | 12.1–23.6 |

Skull Measurements

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 94 | 85 | 94 | 91 | 91 | 90 |
| **$\bar{X}$** | 18.6 | 9.8 | 4.3 | 5.7 | 7.0 | 7.8 |
| **SD** | 0.62 | 0.29 | 0.18 | 0.21 | 0.22 | 0.27 |
| **CV** | 3.34 | 3.00 | 4.33 | 3.75 | 3.19 | 3.50 |
| **OR** | 17.0–19.9 | 9.0–10.6 | 3.9–4.8 | 5.2–6.4 | 6.4–7.8 | 7.2–8.6 |

### Description (Colour Plate II)

Size medium to large; wingspan 32–39 cm. Fur brown, darker above, lighter below, varying considerably from pale to dark, basal half of fur blackish; hairs relatively long, approximately 12 mm on back, fur extending one-third to one-quarter down dorsal surface of uropatagium. Flight membranes and ears blackish. Ears short, barely reaching nostril when laid forward. Pararhinal glands well developed. Foot about half as long as tibia, dorsal side of toes with a few bristle-like hairs. Calcar keeled, extending a little less than halfway down edge of uropatagium; two terminal caudal vertebrae, protruding about 5 mm from uropatagium. Skull massive, with relatively short and broad rostrum and a pronounced sagittal crest. Baculum very small relative to the overall size of bat (approximately 0.9 mm), arrow-shaped (Figure 31, Table 4).

Similar Species: *E. fuscus* can be distinguished from all native brown bats by size.

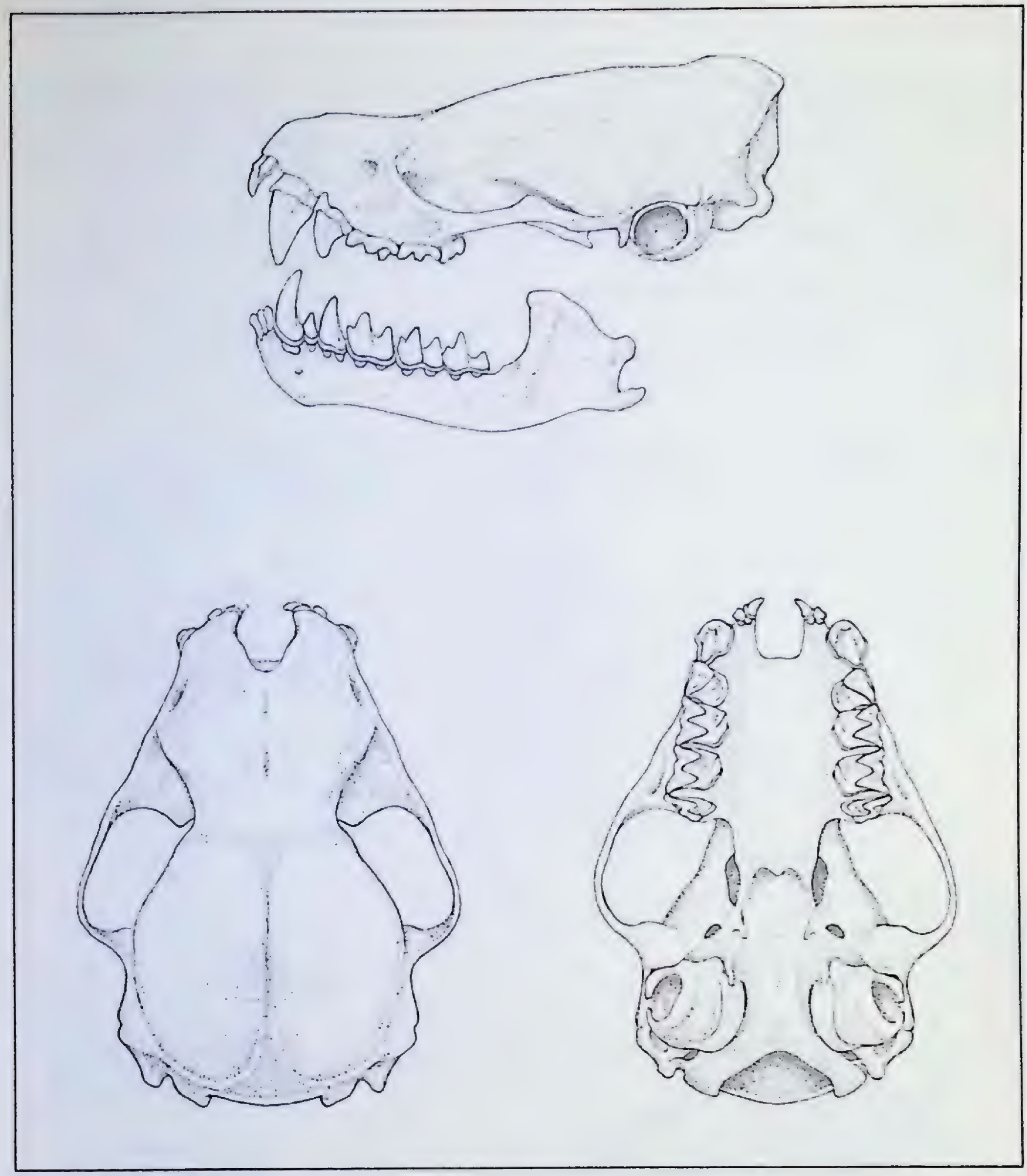

Figure 48. Skull of *Eptesicus fuscus*

## Distribution

The big brown bat is a common and widespread species in Canada. Peripheral localities: *Alberta*: (1) Pine Lake, Wood Buffalo National Park. *British Columbia*: (2) Charlie Lake; (3) Prince George; (4) Stuie; (5) Alberni; (6) Victoria. *Manitoba*: (7) Cedar Lake, 112 km SE of The Pas; (8) Whiteshell Provincial Park. *New Brunswick*: (9) Saint John; (10) St. Andrews. *Ontario*: (11) Sioux Lookout; (12) Schreiber; (13) Hwy. 17 N of Sault Ste Marie; (14) Bigwood. *Quebec*: (15) 11 km NW of Kazabazua; (16) Mont-Saint-Hilaire. *Saskatchewan*: (17) Battleford.

The North American range of the species extends over most of the continent from southeastern Alaska to northern South America and the Caribbean Islands.


Distribution of *Eptesicus fuscus*

## Systematics

Ten subspecies have been described in North America, of which three occur in Canada. The subspecies found here show considerable overlap in cranial and postcranial variables. (For an analysis of geographic variation in this species see Burnett [8]).

*E. f. fuscus* Palisot de Beauvois, 1796, Catalogue raisonné du muséum de Mr. C.W. Peale, Philadelphia, p. 18.
A dark-brown form. Distribution: eastern Canada west to Manitoba.

*E. f. pallidus* Young, 1908, Proc. Acad. Nat. Sci. Phila. 60:408.
A pale-coloured form. Distribution: the prairie provinces.

*E. f. bernardinus* Rhoads, 1902, Proc. Acad. Nat. Sci. Phila. 53:619.
A dull-brown form. Distribution: British Columbia.

## Biology

Habitat

The big brown bat is found in a wide variety of wooded and semi-open habitats. This species is closely associated with buildings and, with *M. lucifugus*, it is the most common bat in larger cities. Summer roosts are in buildings and natural sites such as hollow trees and crevices in rock faces. Maternity colonies have been found in attics, barns and occasionally in tree cavities. This species tends to select cooler places in summer than *M. lucifugus*. Caves and mines are used for hibernation [14, 22, 32], but considerable numbers hibernate in buildings or other man-made structures such as sewers [18].

Food

This species, with its powerful jaw musculature and robust teeth, preys on a wide variety of larger insects, but appears to favour Coleoptera (mostly scarabaeids, June beetles and related species) [4, 21]. Other insects taken include Hemiptera, Hymenoptera, Diptera, Plecoptera, and a few Lepidoptera.

Predators

Predation by avian and mammalian predators appears to be infrequent and is probably not a major cause of mortality [26, 31].

Population

Although this is a common bat in many parts of Canada, little is known about the structure and dynamics of populations of the species here. Studies in the United States estimated prenatal mortality at 34% [27] and preweaning mortality at 7% [10]. Unaged [2, 18] and known-age cohort analyses [11] show evidence of low survival of young and increased survival rate with an increase in age. Survival is highest during the middle age and lower toward the end of the life span. The greatest longevity published is 19 years for a male [23]. The sex ratio at birth is equal. Sex ratios obtained in hibernacula in our latitude generally show a preponderance of males [29], which may not reflect an actual difference in the number of males and females in the population, but a difference in hibernation behaviour of the sexes. However, significant differences were found in the annual survival rates of males and females (0.697 and 0.465 respectively) in Ontario [24] which could account for the observed sex ratios.

This species may regulate the size of its own populations, as at high population numbers a significantly reduced number of young are raised [30].

Activity and Behaviour

The big brown bat emerges early at twilight. There is an initial foraging period within 5 hours after sunset [26], after which the bats retire to night roosts. Foraging activity declines after the initial period throughout the rest of the night. Under favourable conditions big brown bats may fill their stomachs in less than 20 minutes.

The flight of this bat is strong, direct and moderately fast, and usually 7 to 10 m above the ground, as it forages among and over the tops of trees rather than under the canopy. Over streams, *E. fuscus* flew at a greater height and further from the bank than *M. lucifugus* (median height 4.9 and 1.5 m and median distance from bank 2.7 and 0.9 m respectively) [28].

The echolocation calls of *E. fuscus* consist of shallow FM sweeps of medium frequency (Table 3; Figure 9) and high intensity, which allow it to detect a 19 mm sphere up to a distance of 5 m [25]. In addition it has been demonstrated that this species is capable of detecting relatively low-frequency sound, such as that produced by groups of insects, over a maximum distance of at least 600 m [6]. Such long distance acoustic cues could help the bat locate concentrations of flying insects and thus supplement the shorter range high frequency echolocation. Visual cues, such as the glow after sunset [7] are used in orientation.

Big brown bats form maternity colonies of up to 200 individuals or more, although most colonies average less than 100 [12, 36]. During hibernation they are less gregarious and are usually found singly or in small clusters of three or four. Females are most often found alone, whereas males tend to occur more often in clusters. Banding studies have revealed that the big brown bat is a comparatively sedentary species, moving within a relatively small area. In one study only a small number of bats were recaptured away from the banding site at distances varying from 0.8 to 98 km with an average of about 12 km [1]. Movements around 200 km or more have been reported, but are probably unusual [5, 30, 39]. It seems likely therefore that most big brown bats hibernate in the vicinity of their summer haunts. *E. fuscus* is a very hardy bat [1, 18, 36] that does not appear at the hibernacula in substantial numbers until the increasingly inclement weather of approaching winter impels it. In the hibernacula, *E. fuscus* selects cooler and drier sites than *M. lucifugus* [14, 22, 32]. Even after the population has entered hibernation, there is intermittent activity and during mild spells movements between hibernacula may occur.

Reproduction and Ontogeny

Mating takes place in fall and occasionally throughout winter. The time of parturition is variable but most births occur in late June and early July [36]. The female often produces four or more ova [40] but normally bears one or two young. In eastern North America the litter size is usually two, in the west one.

The young are born in a comparatively altricial condition, naked, with closed eyes and ears, weighing about 3 g and with forearm length of about 16.8 mm [9]. Growth is relatively rapid

(forearm 0.8–1.4 mm/day, weight 0.3–0.47 g/day) [9]. The newborn only produces one type of vocalization, the so-called i or isolation call, which the young utters when it is not on the mother and which allows her to locate her offspring [19, 20]. A mother nurses only her own young. During the third week of life the young bat begins to emit the double note (DN) call which is also uttered by the female and helps to bring the two together. By four weeks the young are foraging and at the age of approximately 70 days they attain adult size. Males become sexually mature in their first fall, but only 50 to 75 per cent of the young females do so.

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## Genus *Nycticeius* Rafinesque, 1819
(f. Gk *nux*, genit. *nuktos* night; *eius* suffix meaning belonging to)

Externally *Nycticeius* resembles a small *Eptesicus*. It has a blunt muzzle and ears that are rounded and shorter than those of *Myotis*. The tragus is short and blunt and bent forward. The skull is low and broad and has only one upper incisor and premolar. The number of teeth is 30. Dental formula i1/3; c1/2; p1/2; m3/3.

The genus comprises approximately six species and is distributed in North America, Africa, and the Autralasian area. One or possibly two species are found in North America. Analysis of chromosomal banding patterns of North American vespertilionids suggests that *Nycticeius* is related to *Eptesicus* and *Antrozous* [1].

### References

[1] Bickham, J.W., 1979
[2] Miller, G.S., Jr., 1897*a*

## *Nycticeius humeralis* (Rafinesque)
(f. L *humerus* shoulder)

**Evening Bat** | **Chauve-souris vespérale**

1818 *Vespertilio humeralis* Rafinesque, Am. Monthly Mag. III, p. 445
1819 *Nycticeius humeralis* Rafinesque, J. Physiol. (Paris) LXXXVIII, p. 417
Type locality: Kentucky

External Measurements, Weight and Length of Skull

| | TL | T | HF | FA | E | W | SL |
|---|---|---|---|---|---|---|---|
| OR | 88–105 | 36–41 | 6.5–7.7 | 34–39 | 9–14 | 6–12 | 14–14.7 |

### Description (not illustrated)

A medium-sized bat, lacking distinctive external features; wingspan 26–28 cm. Pelage dull brownish, tips of dorsal hair ash grey, basal portion dark brown, short, approximately 6 mm on back. Patagia and ears blackish. Ears small, rounded, thick and leathery; tragus short, blunt and broad. Foot slightly more than half as long as tibia. Calcar not keeled. Flight membranes thick and leathery. Skull broad and low, with only one upper incisor on each side, separated from canine by a gap. Baculum large relative to the overall size of bat (approximately 2 mm long), blade-like, distal portion deep, with convex walls, terminating in ascending point, proximal end deep. Chromosomes 2N = 46; FN = 48 [1].

Similar Species: *Eptesicus fuscus* is larger and has keeled calcar. *Myotis* species have longer, more slender tragus.

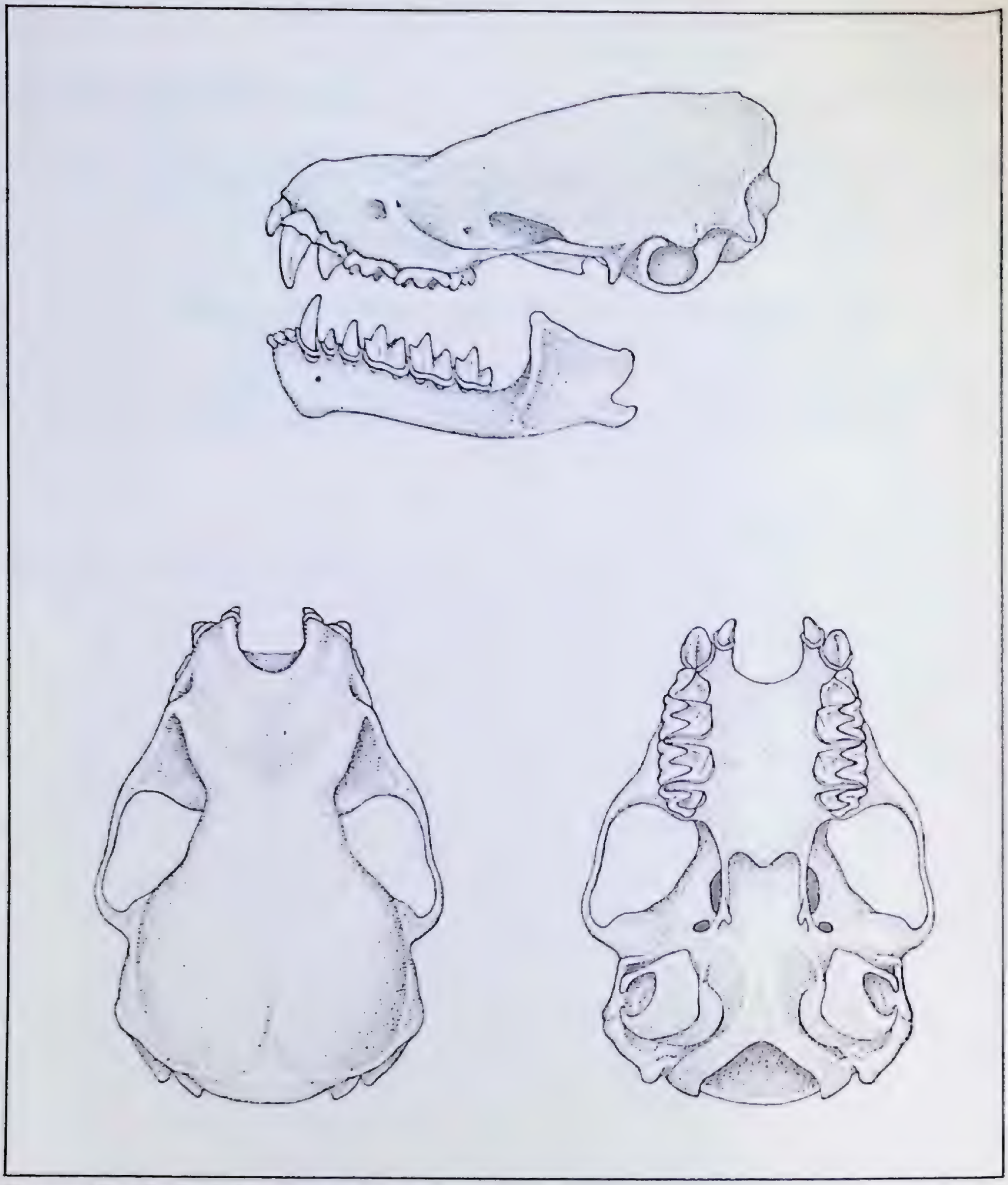

Figure 49. Skull of *Nycticeius humeralis*

## Distribution

This species has been recorded only once in Canada, when a specimen was taken at Point Pelee in May 1911. *N. humeralis* is a predominantly southern species with a wide distribution in the eastern United States south to Florida and the Gulf of Mexico and west to Arkansas, southern Texas and extreme northeastern Mexico.

Distribution of *Nycticeius humeralis*

## Systematics

Three subspecies are recognized. The typical subspecies *N. h. humeralis* has been recorded from Canada. A closely related form, *N. cubanus*, recently relegated to subspecific status in *N. humeralis*, is only known from Cuba [2].

## Biology

In summer the evening bat roosts in buildings or tree cavities. This bat has been reported from a cave only once. Northern populations of this bat are migratory [3], but nothing is known about its life in winter. Habitat

This species appears to be a generalized feeder, preying on a variety of insects (Coleoptera, Lepidoptera, Hemiptera, Homoptera, and Diptera) [5]. It emerges early and flies slowly following a direct course. When it is still light it flies high (up to 30 m) and descends to forage closer to the ground as darkness falls. Females form maternity colonies in trees, under loose bark or cavities, or in buildings. In buildings these colonies may comprise hundreds of individuals, in natural sites probably fewer. The general reproductive pattern is similar to that of other northern vespertilionids. The young, usually two per female, are born around mid-June in the northern part of their range. The newborn young are naked and pink in colour except for the darkly pigmented feet, patagia, ears and lips; the forearm is approximately 14 mm long. Females nurse their own offspring until they are two weeks old, after that they will nurse any young indiscriminately until weaning [4]. Weaning and the beginning of independent foraging occur when the young bat is about four weeks old.

Food

Activity and Behaviour

Reproduction and Ontogeny

**References**


[1] Baker, R.J., and J.L. Patton, 1967
[2] Honacki, J.H., K.E. Kinman, and J.W. Koeppl, 1982
[3] Watkins, L.C., 1972
[4] Watkins, L.C., and K.A. Shump, Jr., 1981
[5] Whitaker, J.O., Jr., 1972

## Genus *Antrozous* H. Allen, 1862
(f. Gk *antron* cave; *zōon* animal)

This genus is characterized externally by large, separate ears, and a truncate muzzle with horseshoe-shaped ridge surrounding the nostrils. The penis is different from that of other North American vespertilionid genera, in being a trilobate structure rather than a simple, roughly cylindrical one.

There are 28 teeth. Dental formula i1/2; c1/1; p1/2; m3/3. The fur is short and woolly. There are two mammae. The three species of *Antrozous* are distributed in western North America (*A. pallidus*), the Tres Marías Islands (Mexico) and Central America (*A. dubiaquercus*) and Cuba (*A. koopmani*). *A. dubiaquercus* is placed in a separate genus, *Bauerus*, by some [2]. It is customary to include *Antrozous* in the subfamily Nyctophilinae with the genera *Nyctophilus*, *Lamingtonia* and *Pharotis*, from Australia and New Guinea. Recent evidence suggests that it may not be closely related to the nyctophilines [3]. It is suggested on the basis of resemblance in the structure of the penis and other morphological characters that *Antrozous* may be most closely related to the Old World genus *Otonycteris*. Analysis of chromosomal banding patterns of North American vespertilionids further suggests that *Antrozous* evolved from an ancestor with a karyotype like that of *Eptesicus* as did *Nycticeius* and the tropical American genus *Rhogeessa* [1]. In view of this evidence *Antrozous* is here regarded as a member of the Vespertilioninae.

### References

[1] Bickham, J.W., 1979
[2] Martin, C.D., and D.J. Schmidly, 1982
[3] Pine, R.H., D.C. Carter, and R.K. LaVal, 1971

## *Antrozous pallidus* (Le Conte)

(f. L *pallidus* pale)

**Pallid Bat** — **Chauve-souris blonde**

1856 *V* [*espertilio*]. *pallidus* Le Conte, Proc. Acad. Nat. Sci. Phila. 7:437
1864 *Antrozous pallidus*, H. Allen, Monogr. Bats N. Am., Smithson. Misc. Collect. 7 (publ. 165):68
Type locality: El Paso, El Paso County, Texas

### External Measurements and Weight

Two males from the Okanagan Valley had the following measurements and weights: TL 115, 121; T 46, 51; HF 11, 11; FA 54, 58; E 30, 28; W 18.6, 22.6. Observed ranges for these measurements for animals of both sexes from California, based on Orr 1954 are: TL 107–130; T 35–49; HF 11–16; FA 53–60, E 26–33; W 20–35 (lowest and highest seasonal means).

### Skull Measurements*

| | SL | MW | IOW | CD | MTL | M3M3W |
|---|---|---|---|---|---|---|
| **N** | 5 | 5 | 5 | 5 | 5 | 5 |
| **$\bar{X}$** | 21.0 | 10.3 | 4.2 | 6.4 | 7.6 | 8.4 |
| **SD** | 1.00 | 0.31 | 0.16 | 0.33 | 0.32 | 0.14 |
| **CV** | 4.77 | 3.06 | 4.04 | 5.09 | 4.28 | 1.73 |
| **OR** | 19.8–22.5 | 9.9–10.8 | 4.0–4.4 | 6.1–6.8 | 7.2–8.0 | 8.2–8.6 |

*Specimens from the southwestern United States

### Description (Colour Plate IV)

A large, pale-coloured, large-eared bat; females slightly larger than males; wingspan 37–39 cm. Fur relatively short (8 mm on the back) and thin; hairs light yellowish with darker brown or grey tips; underparts creamy white. Patagia thick and leathery, pale brownish in colour. Ears pale, extending 20 mm beyond nose when pressed forward, not fused at their bases; tragus long (approximately one-third of ear length) straight and slender with weakly serrated outer edge. Snout truncate with prominent glandular swellings on either side, secretion with a strong distinctive odour, rhinarium scroll-shaped. Eye relatively large. Foot approximately half as long as tibia, calcar extends a little less than halfway along edge of uropatagium, bearing a small terminal lobe. Wings broad, metacarpals approximately equal or third slightly longer than fourth and fifth. Skull large with massive teeth, one upper incisor on each side. Penis quite different from other North American vespertilionids with distal third dorso-ventrally compressed and laterally expanded with three raised, hairy and somewhat wrinkled lobes (Figure 51). Baculum in dorsal aspect wedge-shaped; in lateral aspect saddle-shaped (Figure 31); length of baculum approximately 1 mm. Chromosomes 2N = 46, FN = 50 [2].

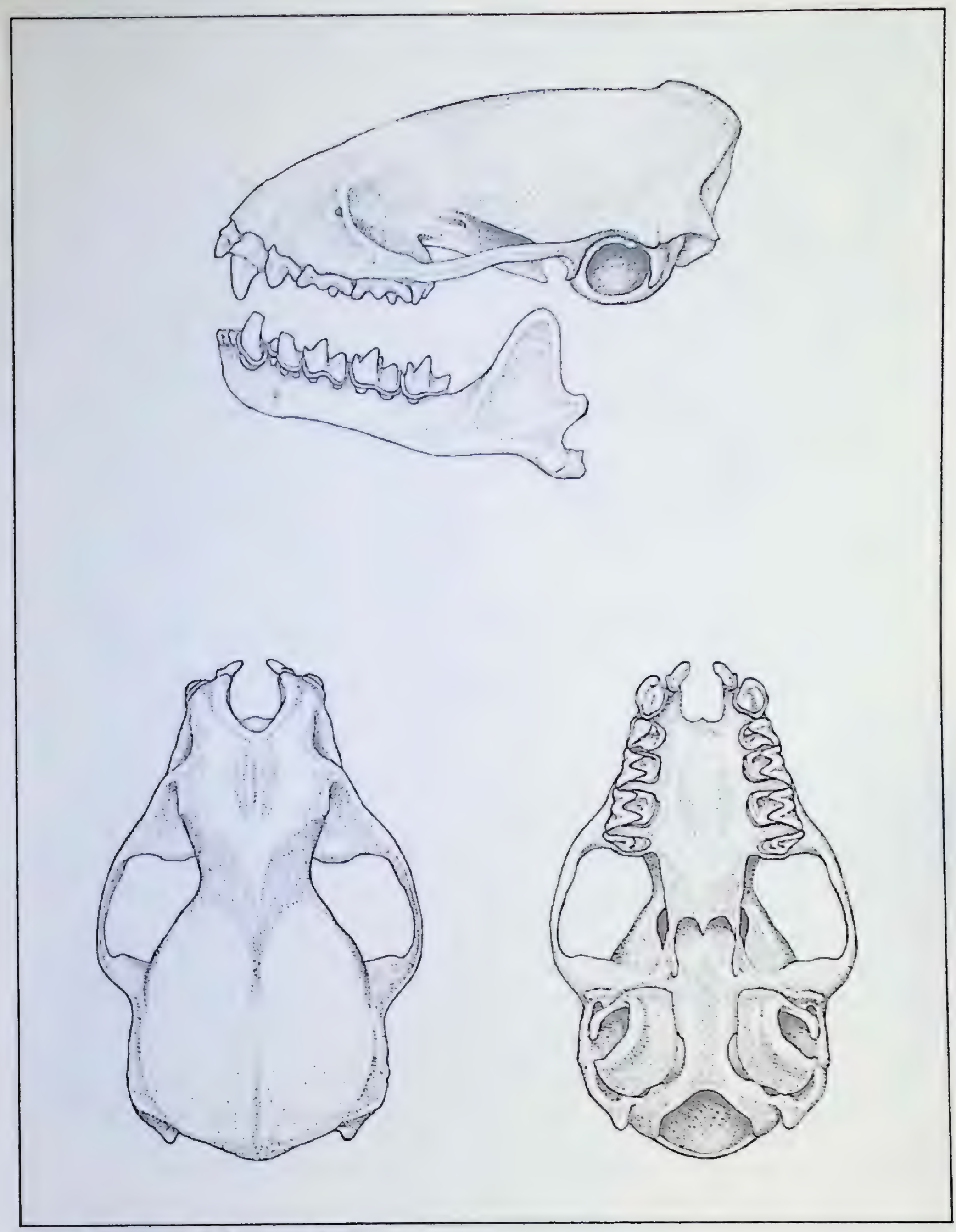

Figure 50. Skull of *Antrozous pallidus*

Similar Species: The pallid bat is not readily confused with any other native species. *Plecotus townsendii* is smaller and has prominent lumps on the snout, and dark basal fur.

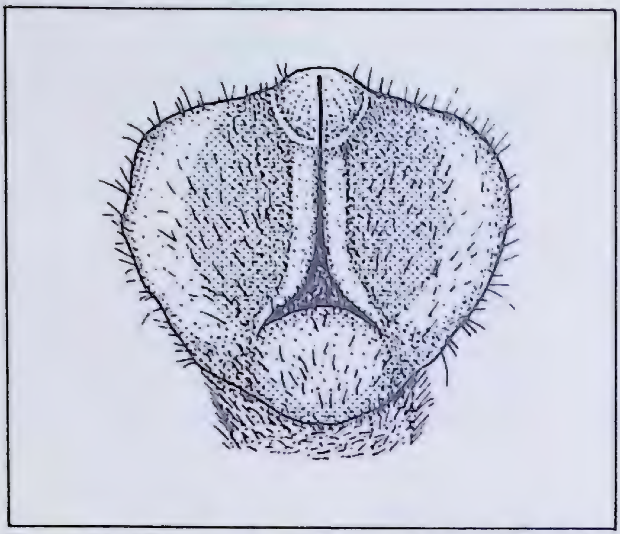

Figure 51. Glans penis of *Antrozous pallidus* (after Martin and Schmidly 1982)

## Distribution

The pallid bat has a very limited distribution in Canada, where it is restricted to the southern Okanagan Valley. The species was first recorded from this area in 1931 [9], when a single individual was collected from a stone pile approximately 5 km north of Oliver. Anderson [1] mentions another one reported taken at Okanagan Landing in 1935. This report has apparently never been confirmed. A dying female was found in Okanagan Falls in 1974. During a survey of the area in 1979 two males were captured and released near Vaseux Lake between Oliver and Okanagan Falls [12]. Further evidence accumulated since then has clearly demonstrated the presence of a resident breeding population in the Okanagan Valley. Peripheral localities: *British Columbia*: (1) see the localities listed above.

The pallid bat's range extends southwards into the western United States, south to Central Mexico.

## Systematics

Five subspecies are recognized [16]. The Canadian population belongs to the subspecies *A. p. pallidus* (Le Conte). See also comments on the relationships of the genus.

## Biology

Little is known about the biology of this bat in Canada, but the species has been studied in the United States. The pallid bat inhabits arid areas with rocky outcroppings and a dominant vegetation of xerophytic shrubs, as well as adjacent dry forest com- Habitat

Distribution of *Antrozous pallidus*

munities [17]. The distributional range of the pallid bat in British Columbia is characterized by hot summers, mild winters and an average annual precipitation of less than 200 mm. The typical xerophytic vegetation of the area includes antelope-bush (*Purshia tridentata*), sagebrush (*Artemisia tridentata*), rabbit-bush (*Begelowia graveolens*) and cactus (*Opuntia polyacantha*). Forested habitat consists of riparian forest along the lakeshores and streams, and dry forest dominated by ponderosa pine (*Pinus ponderosa*) on the lower slopes. All known captures of pallid bats in British Columbia were at elevations of less than 500 m. Preferred daytime roosts are in rock crevices and buildings [17, 22]. For night roosts it selects open shelters that are easily approached, such as porches, bridges and cave or mine entrances.

Food

*Antrozous* is capable of chewing hard prey and feeds on many different kinds of medium to large arthropods, with body lengths of 2 cm or more, including, in addition to moths, substantial numbers of ground dwelling and flightless forms such as crickets, grasshoppers, beetles and scorpions [5, 6, 7, 11, 13, 17, 19, 23]. Small vertebrates (e.g. a small lizard (*Phrynosoma douglassi*) [18] and a pocket mouse (*Perognathus flavus*) [5]) may occasionally be

captured and eaten and Howell [14] presents evidence that *A. pallidus* may occasionally eat the fruit of the organ pipe cactus (*Lemaireocereus thurberi*) in Arizona. The fruit appears to be ingested incidentally when the bat attempts to capture moths attracted to the fruit and illustrates how fruit eating in bats may have evolved.

Population

Nothing is known about population structure and dynamics in Canada.

Activity and Behaviour

The pallid bat emerges quite late in the evening, from 24 minutes to nearly an hour after sunset, depending on the time of year. Time of emergence is later in summer than in spring or fall. In central Arizona this species has two main foraging periods with an interlude spent at a night roost [18]. After the initial foraging period these bats gather in clusters at night roosts where they may go into torpor depending on the season. The timing and lengths of foraging flights vary with the season. In the cool seasons, spring and autumn, emergence is slower, and the time spent foraging is shorter and more time is spent in the night roosts. In the warm months of summer, emergence is later, but foraging times are longer and less time is spent in night roosts. The flight of this bat, which is comparatively more noisy than that of other native bats, is usually low, 0.5–2.5 m above the ground [18], and relatively slow. Brief periods of hovering and short glides have been observed [17]. The number of wingbeats per second is 10 to 11 in straight flight, which is considerably fewer than that of the smaller species in its range (about 15 strokes per second). The pallid bat also lacks the manoeuvrability of its smaller relatives. It lands head-up on vertical surfaces and, having found a secure footing, pivots around by releasing the hold of both thumbs and one foot, which is reattached as soon as the upside-down position has been achieved.

The pallid bat crawls well, supporting its weight on its wrists and feet, and it frequently lands on the ground to capture its prey. When the prey is subdued after a shorter or longer struggle it is carried off. Smaller prey is eaten in flight, but large prey is taken to a night roost, where unpalatable parts, such as wings, head, etc., are discarded and the remainder consumed [5].

Insects are also captured on the surfaces of trees and shrubs and under some circumstances this bat may also pursue its prey in the air. The extent of aerial foraging by this species is not known. Prey is detected by listening for rustling sounds produced when it moves [5]. However the bat ignores the mating calls of crickets and grasshoppers which are, as a rule, given from heavy cover. Echolocation is apparently not used in detecting and capturing prey on the ground, as no sound pulses are emitted during the approach and capture of prey. Echolocation pulses are however emitted in flight and function primarily in orientation, to avoid obstacles and to give the bat information about its surroundings.

The relatively large eyes of this species appear not to be used in detecting prey. Their size suggests that they may play a role

in navigation, but their exact function has yet to be experimentally tested.

The pallid bat is a social species that uses four principal types of vocalization for communication [8, 17]: directives, squabble notes, irritation buzzes and FM echolocation pulses. The "directive" call consists of clear, high-pitched notes uttered in a rapid series of one to five evenly spaced notes (sit, sit, sit), sounding like a short circuit in a power line according to Orr [17]. This call is a means by which individuals communicate their whereabouts to one another and it serves to direct conspecifics to roosts. A lone adult may utter directive calls until answered by others and a mother uses them to respond to her baby's call. This call is heard at dusk when the bats are leaving their roost and again at dawn when they return. It is also heard under similar circumstances at their night roosts. The "squabble" notes, a series of high-pitched (5–15 kHz) dry, rasping double notes, express mild irritation and are thought to function in spacing the bats in their roosts. They are often heard during the day especially when it is warm.

The "irritation buzz" or "intimidation note", an insect-like buzz, is more agonistic and is used both in intra- and interspecific encounters. It is used to threaten and indirectly to alert other bats to potential danger. During weaning it is also used by mothers toward their young. FM echolocation calls consist entirely of ultrasonic sounds and, although primarily used in orientation, they may indirectly communicate the location and activity of individuals to other bats. Other minor sounds are the "contact note" or "note of contentment" uttered when animals, especially mothers and infants, are in physical contact and the "plaintive" note uttered by females in labour and presumably induced by pain.

Summer colonies may number up to 100 individuals and may be composed of adults of both sexes [17, 20, 22]. Less is known about the species' habits in winter, but it appears that it is sedentary and hibernates within or near its summer range.

Reproduction and Ontogeny

Male gonads enlarge toward the latter part of August and decrease from the middle of October to the end of April [17]. In the southwestern United States copulation takes place in October and November and probably intermittently throughout the winter. As in other temperate vespertilionids, sperm is stored in the uterus of the female and fertilization occurs when ovulation takes place in spring. In California, maternity colonies begin to form in late March and early April and the young are born from late April [4] to late June [3] with most births occurring in the first half of June. In southern Arizona most births occur in mid-June [10]. Further north in Kansas, young are born in late June and early July [21]. It appears likely that parturition dates in British Columbia are similar to those in Kansas, but information is thus far lacking.

The gestation period is estimated to be from 53 to 71 days [17]. The female usually gives birth to two (79% of cases), or one and rarely three young. Birth takes place with the female in an upright position and the tail membrane curved forward. The

young are altricial, being born naked, with eyes closed, ears folded close, with a forearm length of 17 mm and weighing around 3 g. The eyes open and ears become erect after 8 to 10 days. The newborn young emits an isolation call whenever it is off the mother's nipple. At first audible, the call gradually increases in frequency beyond the limit of human hearing. It continues to emit this sound until it is three weeks of age. Later it develops a double note (DN) call, which is also emitted by the mother and ensures the reunion of mother and infant after separation. During the first few days after the birth, the female will fly inside the roost with her young attached, but this has not been observed on hunting flights. The mother nurses only her own young which she recognizes by auditory and olfactory cues. The lactating female leaves to forage for short periods of 20 to 30 minutes, after which she returns to feed her young. This pattern may be repeated several times through the night. When the young are six weeks of age they are capable of flight and can take solid food, but mothers and young remain together and forage together in July and August.

The young reach adult size by seven weeks of age, but weigh considerably less than adults [10]. Yearling females weigh less than adult females until after their second year and give birth to only one young. Juvenile males are not sexually active in their first autumn.

**References**


[1] Anderson, R.M., 1946
[2] Baker, R.J., and J.L. Patton, 1967
[3] Barbour, R.W., and W.H. Davis, 1969
[4] Beck, A.J., and R.L. Rudd, 1960
[5] Bell, G.P., 1982
[6] Black, H.L., 1974
[7] Borell, A.E., 1942
[8] Brown, P., 1976
[9] Cowan, I. McT., and C.J. Guiguet, 1965
[10] Davis, R., 1969
[11] Easterla, D.A., and J.O. Whitaker, Jr., 1972
[12] Fenton, M.B., C.G. van Zyll de Jong, G.P. Bell, D.B. Campbell, and M. Laplante, 1980
[13] Hatt, R.T., 1923
[14] Howell, D.J., 1980
[15] Krutzsch, P.H., and T.A. Vaughan, 1955
[16] Martin, C.O., and D.J. Schmidly, 1982
[17] Orr, R.T., 1954
[18] O'Shea, T.J., and T.A. Vaughan, 1977
[19] Ross, A., 1967
[20] Storer, T.I., 1931
[21] Twente, J.W., Jr., 1955
[22] Vaughan, T.A., and T.J. O'Shea, 1976
[23] Whitaker, J.O., Jr., C. Maser, and L.E. Keller, 1977

## Family MOLOSSIDAE Gill, 1872

(f. L *molossus* Molossian hound,
a mastiff-like breed of dog used by shepherds)

**Free-tailed bats** **Molossidés**

Small to large bats (FA 30–73) characterized by broad muzzles with nostrils opening on a pad, large lips; upper lip often with vertical furrows. Ears usually large and broad, often fused across forehead, tragus small and antitragus usually large. Wings long and narrow, membranes thick and leathery, uropatagium not extensive, tail projecting far beyond it. Legs short, strong and muscular, feet short and broad. First and fifth toes possessing thickened skin along their edges with dense long bristles. Metacarpal of second finger well developed with one rudimentary phalanx, third finger with third phalanx cartilaginous except for the extreme basal part, at rest first phalanx flexed on upper side of metacarpal. Skull with narrow gap between premaxillae. Teeth 26 to 32 with cusp pattern similar to that of vespertilionids.

The Molossidae comprise 12 genera and approximately 86 species, and are widely distributed in the tropical and subtropical regions around the world. The earliest fossil molossids date back to the European Oligocene.

### References

[1] Freeman, P.W., 1981*b*
[2] Miller, G.S., Jr., 1907

## Genus *Tadarida* Rafinesque, 1814*

(f. NL *tadarida*, a word coined by Rafinesque, the derivation and possible meaning were not revealed by him. According to Barbour and Davis, 1969, the name means "withered toad" but they do not give the etymology of the word.)

Deep vertical grooves on the upper lip, narrow separation of the premaxillae and the Z-shaped cusp-pattern of M3 characterize this genus. The genus has about 21 species and is found in the Old and New World.

*Freeman 1981 has proposed that the New World *Tadarida*, except for *T. brasiliensis* be placed in a separate genus *Nyctinomops* Miller, 1902, Proc. Acad. Nat. Sci. Phila. 54, p. 393.

## *Tadarida macrotis* (Gray)

(f. Gk *makros* big; *ous* genit. *ōtos* ear)

**Big Free-tailed Bat** **Grand Molosse**

1839 *Nyctinomus macrotis* Gray, Ann. Nat. Hist. 4:5
1949 *Tadarida molossa*, Hershkovitz, Proc. U.S. Nat. Mus. 99:452
1962 *Tadarida macrotis* Husson, The bats of Surinam, Zool. Verh. (Leiden), p. 236
Type locality: Cuba

### External Measurements

The single specimen collected in Canada had the following measurements: TL 139; T 52; HF 13.

### Description (not illustrated)

A large bat (FA 58–64) with tail extending 2.5 cm or more beyond uropatagium; wingspan 42–44 cm. Fur short, glossy, light reddish-brown to dark brown or black; hairs lighter, nearly white at the base. Ears large, fused basally. Skull large (SL 22–24), with narrow gap between premaxillae, long interorbital area with nearly parallel outline when viewed dorsally.

Similar Species: This bat is unlike any other native species.

### Distribution

Accidental in Canada where it is known from only one specimen collected in November 1938 [1] at Essondale, New Westminster, British Columbia. The range of this species includes South America, the Caribbean area, Central America, Mexico and the southwestern United States, where it is locally common. This strong flier has been recorded from widely scattered localities far beyond its normal breeding range, particularly in late summer and fall after the dispersal of summer colonies.

Distribution of *Tadarida macrotis*

## Biology

Not much is known about the biology of this species. It inhabits rocky country, where it roosts in crevices high up the cliff faces. This bat leaves its roost late, when it is quite dark. The flight of the big free-tailed bat is fast and powerful. Food appears to consist almost entirely of large moths [2, 4]. Maternity colonies are formed by the females, who give birth to a single young. As the species is incapable of hibernation, the northern populations are probably migratory. In Utah, in the northern part of the species' distributional range, individuals were captured from the latter half of May to the middle of September, but none were captured in winter [3].

## References

[1] Cowan, I. McT., 1945
[2] Easterla, D.A., and J.O. Whitaker, Jr., 1972
[3] Poché, R.M., 1979
[4] Ross, A., 1967

# GLOSSARY

**A** – See "Acrocentric".
**Acrocentric**
(Gk *akros* tip; *kentron* centre)
Rod-shaped chromosome with centromere at one end.
**Airfoil**
Shaped surface such as a wing, convex on top, concave below, which produces lift and drag when moved through air.
**Altricial**
(L *altrisc* nourisher)
Applies to young born in a very immature condition, requiring a high degree of parental (usually maternal) care.
**Antebrachial membrane**
(L *ante* before; *brachium* arm)
See "propatagium".
**Antitragus**
(Gk *anti* opposite; *tragos* goat)
Projection opposite the tragus of the external ear.
**Aorist**
(Gk *aoristos* indefinite)
A Greek grammatical tense denoting action in the past.
**Aposematic**
(Gk *apo* away; *sema* signal)
Referring to warning colours, which function to scare enemies.
**Aspect ratio**
The ratio of length to width of a wing, high aspect ratio is associated with rapid flight, low aspect ratio with slow, manoeuvrable flight.
**Autosome**
(Gk *autos* self; *sōma* body)
Chromosome that is not a sex chromosome.
**Axillary**
(L *axilla* armpit)
In the armpit.

**Baculum**
(L *baculum* rod)
Penis bone, skeleton of the penis found in some insectivores (Tenrecidae, Talpidae), bats, rodents, carnivores and primates (except man).
**Bicornate**
(L *bis* twice; *cornu* horn)
With two horn-like processes.
**Boreal Forest**
Continuous belt of primarily coniferous forest stretching from Newfoundland and Labrador to the Rocky Mountains and Alaska (see inside front cover).
**Broadband signal**
Echolocation call with a wide range of frequencies.

**Calcar**
(L *calcar* spur)
Process of calcaneus (heel bone), which supports the uropatagium (interfemoral or tail membrane) between the foot and the tail.
**Camber**
The convexity of the wing.
**Canine (caniniform)**
(L *caninus* pertaining to dog)
Dog- or eye-tooth.
**CD** - See "Cranial depth".
**Centromere**
(Gk *kentron* centre; *meros* part)
Part of the chromosome located on the equator of the spindle at metaphase and dividing at anaphase, site of spindle attachment and controlling chromosome activity.
**Chiropatagium**
(Gk *kheir* hand; L *patagium* border)
Membranous skin expansion between the fingers of bats.
**Chromosomal banding**
Differentially stained regions of the chromosomes, produced by special histological techniques, which allow one to distinguish between homologous pairs.
**Clavicle**
(L *clavicula* small key)
Collar bone.
**Coitus**
(L *coire* to go together)
Copulation.
**Coleoptera**
(Gk *koleos* sheath; *pteron* wing)
Beetles, an order of the class Insecta.
**Cranial depth (CD)**
The depth from the top of the cranium to the base of the occipital condyles (see Figure 2).

**dB** - See "Decibel".
**Decibel**
A unit for measuring relative intensities of sounds.
**Diphyodont**
(Gk *diphues* twofold; *odous* tooth)
Having deciduous (milk) and permanent sets of teeth.
**Diploid**
(Gk *diplous* double; *eidos* form)
Having a double set of chromosomes, the typical number of chromosomes of a species.
**Diptera**
(Gk *dis* twice; *pteron* wing)
Flies. Order of insects having one pair of wings.
**Discoidal (placenta)**
A deciduate (i.e. the uterine epithelium is destroyed by the embryonic side of the placenta) placenta with a close relationship between maternal and embryonic circulations usually of discoidal shape.

**Distal**
(L *distare* to stand apart)
Farthest from the midline of the animal, or farthest from the point of attachment.
**Doppler shift**
Change in observed frequency of a wave owing to the relative motion between observer and wave source. Sound from a sound source approaching an observer rises in frequency; that from a receding source shifts to a lower frequency.
**Duplex**
(L *duplex* twofold)
Refers to the presence of two separate uteri, a primitive condition in mammals found in marsupials, bats and rodents. In most mammals the distal parts of the uteri are fused forming a bicornuate or bipartite uterus.

**E** – See "Ear length."
**Ear length (E)**
The distance from the notch to the tip of the ear (See Figure 1).
**Echolocation**
(L fr. Gk *ēkhō* echo; L *locare* to place)
Location of objects by means of echoes usually of supersonic sounds.
**Ectoloph**
(Gk *ektos* outside; *lophos* crest)
Ridge connecting paracone to metacone (see Figure 2).
**Electrophoresis**
(Gk *ēlektron* amber; *pherein* to bear)
A process of separating different molecules owing to their different rates of migration in an electric field.
**Enzyme**
(Gk *en* in; *zumē* leaven)
A catalyst produced by living organisms and acting on one or more substances.
**Eocene**
(Gk *ēos* dawn; *kainos* recent)
Division (epoch) of the Tertiary, following the Palaeocene and preceding the Oligocene, lasting from approximately 54,000,000 to 38,000,000 years B.P.
**Epididymis**
(Gk *epi* upon; *didumos* testicle)
A mass of tissue on the testicle, consisting chiefly of vasa efferentia, which connects the testicle with the vas deferens (duct leading to the penis).
**Exocrine gland**
(Gk *exō* outward; *krinein* to separate)
Glands whose secretion is drained by ducts.

**FA** – See "Forearm length".
**Feeding buzz**
Rapid succession of echolocation pulses during the final approach to a target; made audible with the aid of a bat detector, separate pulses coalesce into a buzz.
**FN** – See "Fundamental number".

**Forearm length (FA)**
Distance from the outside of the wrist to the outside of the elbow (see Figure 1).
**Fossil**
(L *fossilis* from *fodere* to dig)
Plant or animal remains preserved in strata of earth, having undergone greater or lesser chemical or physical change.
**Frugivorous**
(L *frux* fruit; *vorare* to devour)
Feeding on fruit.
**Fundamental number (FN)**
The number of chromosome arms in a karyotype; when only the arms of autosomes are counted it is designated as FNa.

**Harmonics**
(Gk *harmonikos)*
Overtones, component frequencies two, three or more times higher than the principal frequency.
**Hemiptera**
(Gk *hemi* half; *pteron* wing)
Bugs, a large order of insects, with piercing mouth parts, usually two pairs of wings, anterior harder than posterior.
**Heterodont**
(Gk *heteros* other; *odous* tooth)
Having teeth differentiated for different functions.
**Heterothermic**
(Gk *heteros* other; *thermē* heat)
Applies to animals with a type of temperature regulation that allows them to vary their body temperature with that of the surrounding medium.
**HF** – See "Hind foot length".
**Hibernaculum**
(L *hibernaculum* winter quarters)
Place where animals hibernate.
**Hibernation**
(L *hibernus* wintry)
To pass the winter in a resting state accompanied by physiological changes, most importantly an alteration of temperature regulation that makes the animal poikilothermic usually down to temperatures a little above 0°C.
**Hind foot length (HF)**
Distance from the end of the heel bone to the end of the claw on longest toe (see Figure 1).
**Holarctic**
(Gk *holos* whole; *arktos* bear)
Zoogeographical region including the northern part of the Old and New World.
**Homeotherm**
(Gk *homoios* alike; *thermē* heat)
An animal that maintains a constant body temperature within narrow limits, independent of the temperature of the surroundings.
**Homoptera**
(Gk *homoios* alike; *pteron* wing)
An order of insects, with piercing mouth parts and two pairs of wings that are alike. This order includes leafhoppers and aphids among others.

**Hymenoptera**
(Gk *humen* membrane; *pteron* wing)
Order of insects with two pairs of membranous wings, which are coupled together; including ants, wasps, bees and sawflies.
**Hypocone**
(Gk *hupo* under; *kōnos* cone)
Posterior internal cusp of upper molar (see Figure 2).
**Hypoconid**
(Gk *hupo* under; *kōnos* cone)
Posterior buccal cusp of lower molar (see Figure 2).

**Incisor**
(L *incisus* cut into)
Teeth in the premaxillae and their opposites in the mandible.
**Inguinal**
(L *inguen* groin)
In or near the groin.
**Interfemoral membrane** – See "uropatagium".
**Interorbital width (IOW)**
The least width between the orbits (see Figure 2).
**IOW** – See "Interorbital width".
**Isoptera**
(Gk *isos* equal; *pteron* wing)
Order of insects including the termites.

**Karyotype**
(Gk *karuon* nucleus; *tupos* pattern)
Chromosome complement (size, shape, and number) of a somatic cell.
**kHz**
Kilohertz, unit of frequency equal to 1000 cycles per second.

**Lepidoptera**
(Gk *lepis* scale; *pteron* wing)
Order of insects including butterflies and moths.

**M** – See "Metacentric".
**Mammae**
(L *mamma* breast)
Milk-secreting organ.
**Mastoid width (MW)**
Distance across the mastoids (see Figure 2).
**Maxillary toothrow length (MTL)**
The distance from the anterior part of the upper canine to the posterior part of the last upper molar (see Figure 2).
**Mesostyle**
(Gk *mesos* middle; *stulos* pillar)
Vertical buccal ridge in the middle of upper molar (see Figure 2).
**Metacentric**
Referring to the central position of the centromere on the chromosome.
**Metacone**
(Gk *meta* after; *kōnos* cone)
Posterior external cusp of upper molar (see Figure 2).

**Metaconid**
(Gk *meta* after; *kōnos* cone)
Posterior internal cusp of lower molar (see Figure 2).
**Metaloph**
(Gk *meta* after; *lophos* crest)
Posterior crest of molar connecting metacone, metaconule and hypocone (see Figure 2).
**Metastyle**
(Gk *meta* after; *stulos* pillar)
Posterior vertical buccal ridge of upper molar (see Figure 2).
**Molar**
(L *molere* to grind)
Teeth adapted for grinding or crushing; they are not preceded by milk-teeth.
**Monoestrous**
(Gk *monos* single; *oistros* gadfly)
Having one oestrus or heat period in a breeding season.
**Monophyletic**
(Gk *monos* single; *phulē* tribe)
(Of two or more species, or a higher taxon) descended from the same immediate ancestral taxon.
**Monotypic**
(Gk *monos* single; *tupos* type)
Taxon containing only one immediately subordinate taxon (i.e. a genus with one species, or a species containing one subspecies).
MTL - See "Maxillary toothrow length".
MW - See "Mastoid width".

2N - See "Diploid (number)".
**Narrow band signal**
Echolocation call with a narrow range of frequencies.
**Neuroptera**
(Gk *neuron* nerve; *pteron* wing)
Order of insects including alder flies and lacewings.
**Night roost**
Roost used by bats during the night to ingest food brought from nearby feeding areas, to rest after a period of foraging or to serve as a meeting place.
**Nominate form**
A subordinate taxon (e.g. subspecies or subgenus), which contains the type of the subdivided higher taxon and bears the same name (e.g. *Myotis lucifugus lucifugus, Myotis (Myotis) myotis*).

**Palaeocene**
(Gk *palaois* ancient; *kainos* recent)
Earliest division (epoch) of the Tertiary, preceding the Eocene Epoch and following the Cretaceous Period, lasting from approximately 65,000,000 years to 54,000,000 years B.P.
**Paracone**
(Gk *para* beside; *kōnos* cone)
Anterior external cusp of upper molar (see Figure 2).

**Paraconid**
(Gk *para* beside; *kōnos* cone)
Anterior internal cusp of lower molar (see Figure 2).
**Paraloph**
(Gk *para* beside, *lophos* crest)
Short ridge connecting the base of the paracone and the protoconule (see Figure 2).
**Pararhinal glands**
(Gk *para* beside; *rhis* nose)
Exocrine glands on either side of the snout.
**Parastyle**
(Gk *para* beside; *stulos* pillar)
Anterior vertical buccal ridge of upper molar (see Figure 2).
**Pectoral**
(L *pectus* breast)
Pertaining to chest, in the chest region.
**Pectoralis muscle**
Important muscle of the chest with its origin on the sternum and its insertion on a process beneath the proximal end of the humerus.
**Piscivorous**
(L *piscis* fish; *vorare* to devour)
Fish-eating.
**Plagiopatagium**
(Gk *plagios* oblique; L *patagium* border)
Membranous expansion of skin between the last finger and the body.
**Plecoptera**
(Gk *plekō* to twist; *pteron* wing)
An order to insects with aquatic nymphs, adults with long soft bodies and lacy wings folded over the body at rest (stone flies).
**Polytypic**
(Gk *polus* many; *tupos* type)
A taxon containing two or more taxa in the immediately subordinate category.
**Premolar**
(L *prae* before; *mola* mill)
Teeth between the canine and the molars.
**Propatagium**
(Gk *pro* before; L *patagium* border)
Expansion of skin stretched between the forearm and the humerus (see Figure 1).
**Protocone**
(Gk *prōtos* first; kōnos cone)
Inner cusp of upper molar (see Figure 2).
**Protoconid**
(Gk *prōtos* first; *kōnos* cone)
External cusp of upper molar (see Figure 2).
**Protoconule**
(Gk *prōtos* first, *kōnos* cone)
Anterior intermediate cusp of upper molar (see Figure 2).
**Proximal**
(L *proximus* next)
Nearest centre or midline of body or nearest point of attachment.

**Relict**
(L *relictus* abandoned)
Applied to species surviving in an area isolated from the main distributional range, because of historical environmental changes.
**Reproductive (biotic) potential**
The maximum rate of population increase r = b - d where b is the birth rate and d the death rate. The birth rate depends on speed of maturation and fecundity (i.e. number of live offspring produced by a female) of individuals; death rate on the length of life of the individuals.
**Rostrum**
(L *rostrum* beak)
Part of the cranium anterior to the orbits.

**Secodont**
(L *secare* to cut; Gk *odous* tooth)
Having teeth adapted for cutting.
**Skull length**
The distance between the most posterior part of the cranium and the tip of the premaxillae.
**SL** - See 'Skull length''.
**SM** - See ''Submetacentric''.
**Spermatogenesis**
(Gk *sperma* seed; *genesis* origin)
Sperm formation.
**Spermatozoa**
(Gk *sperma* seed; *zōon* animal)
Plural of spermatozoan, a mobile male reproductive cell, consisting of head, middle piece and flagellum.
**ST** - See ''Subtelocentric''.
**Submetacentric**
(L *sub* under; Gk *meta* among; *kentron* centre)
Nearly metacentric.
**Subtelocentric**
(L *sub* under)
Refers to chromosomes that are nearly telocentric.

**T** - See ''Tail length''.
**Tail length (T)**
The length from the base of the tail to the tip of the tail vertebrae.
**Taxon (pl. taxa)**
(Gk *taxis* arrangement)
A taxonomic group that is sufficiently distinct to be named and to be ranked in a definite category.
**Telocentric**
(Gk *tĕlos* end; *kentron* centre)
Chromosome with terminal centromere.
**Tipulids**
Diptera of the family Tipulidae, crane flies.
**TL** - See ''Total length''.
**Total length (TL)**
The distance from the tip of the nose to the tip of the tail (last vertebra).

**Tragus**
(Gk *tragos* goat)
A small projection in front of the ear conch (pinna).
**Trichoptera**
(Gk *thrix* hair; *pteron* wing)
Caddis flies, an order of insects, whose aquatic larvae live in cases made of sand or pieces of vegetation.
**Tritubercular**
(L *tres* three; *tuberculum* small hump)
Molar teeth with three cusps.

**Ultrasonic**
(L *ultra* beyond; *sonare* to sound)
Sound beyond the upper limit of human hearing.
**Ultrasound** – See "ultrasonic".
**Uropatagium**
(Gk *oura* tail; L. *patagium* border)
Membranous skin expansion between the hind legs.

**W** – Weight in grams.
**Wing loading**
The weight divided by the wing area; the lower the wing loading the greater the amount of lifting surface per unit weight, which allows flight at low speeds.

**X-chromosome**
Sex chromosome found paired in the homogametic sex (the female in mammals) and single in the heterogametic sex (the male in mammals).

**Y-chromosome**
The sex chromosome found only in the male. Differs from the X-chromosome usually in being smaller.

**Zeitgeber**
(German *Zeit* time; *geben* to give)
Environmental factor(s) which synchronizes endogenous rhythms with external circadian or circannual cycles.

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# Appendix

Identification of skulls of similar species of *Myotis*

If the use of the key (p. 55) does not lead to a definite identification of an unknown skull of *Myotis* species, the following methods may be used to arrive at a correct identification.

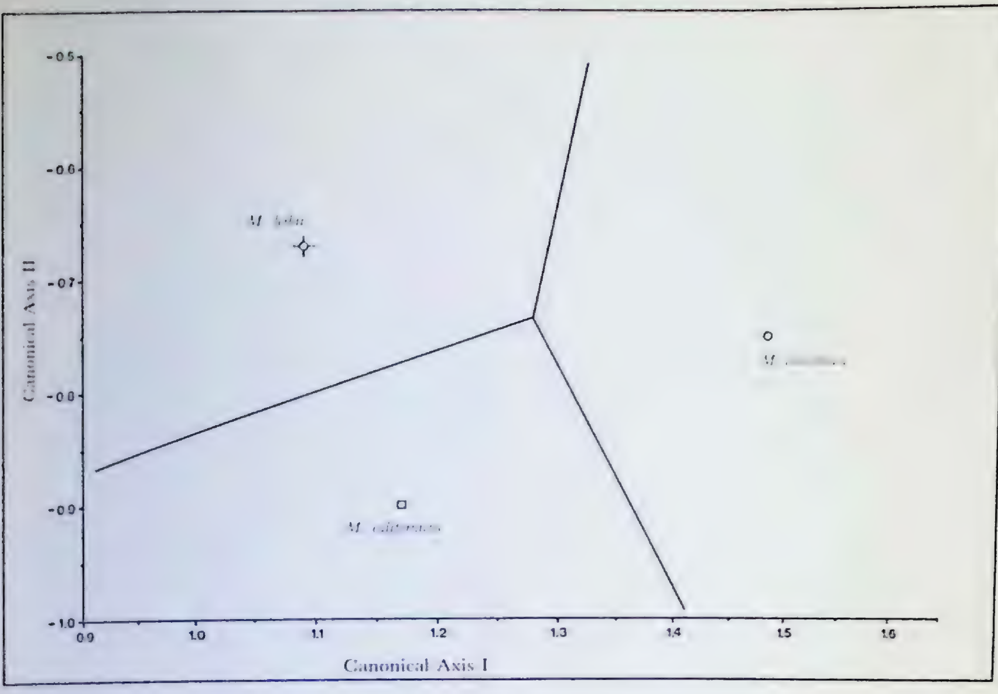
To assign an unknown skull to the correct species, take the measurements indicated for the group you are dealing with (see Figure 2 for definition of measurements). Care should be exercised that measurements are taken accurately. Multiply each measurement by the appropriate discriminant weight and add the products. The resulting total represents the discriminant score of your specimen. Compare the score obtained to the centroids and dividing point between the taxa concerned, and assign it to the species to which it is nearest.

In the case of a three-way discrimination, project the scores for your specimens onto the bivariate plot to determine its identity.

A. Discrimination of skulls of small-footed *Myotis* (*M. leibii, M. ciliolabrum* and *M. californicus*)

| Measurement | Discriminant Weights | |
|---|---|---|
| | Axis I | Axis II |
| IOW | −0.114 | −0.036 |
| OWL | −0.097 | 0.158 |
| M3M3W | 0.028 | −0.159 |
| I3I3W | −0.633 | 0.015 |
| P4M3L | 0.618 | −0.064 |
| CW | 0.214 | 0.859 |
| CD | 0.034 | −0.304 |
| CH | 0.275 | 0.159 |

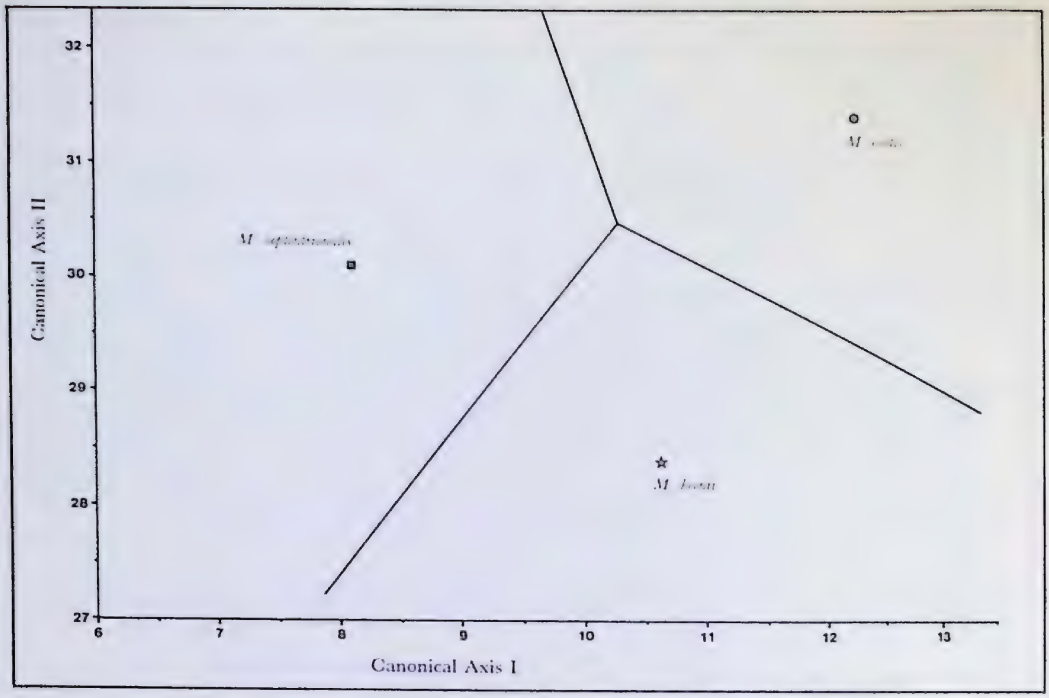
Calculate scores for each axis by multiplying each measurement by the appropriate weight and adding the products. Plot the scores on the graph on p. 211 to arrive at correct identification.




B. Discrimination of skulls of long-eared *Myotis*

| Measurement | Discriminant Weights Axis I | Axis II |
|---|---|---|
| 1. SL | 1.65 | 0.26 |
| 2. MW | − 2.35 | 0.05 |
| 3. OWL | − 0.18 | − 0.12 |
| 4. RW | − 0.52 | 1.98 |
| 5. M3M3W | − 0.17 | 0.54 |
| 6. P2P2W | 0.65 | − 1.18 |
| 7. I3I3W | − 4.19 | 1.44 |
| 8. MTL | − 2.42 | 2.00 |
| 9. P4M3L | 5.12 | − 1.11 |
| 10. M2L | 2.12 | 1.80 |
| 11. M2W | 5.10 | 0.00 |
| 12. CW | − 3.30 | 9.15 |

Calculate scores for each axis by multiplying each measurement by the appropriate weight and adding the products. Plot the scores on the graph on p. 212 to arrive at correct identification.




C. Discrimination between skulls of *Myotis volans* and *M. lucifugus* and *M. yumanensis*

| Measurement | Discriminant Weight |
|---|---|
| SL | − 11.42 |
| MW | 18.78 |
| RW | − 12.70 |
| M3M3W | 0.26 |
| I3I3W | 10.38 |
| P4M3L | 12.04 |
| CD | 10.14 |

Centroid *M. volans* 73.2
Centroid *M. lucifugus* and *M. yumanensis* 59.9

Dividing point between the two groups is 66.6.
If score > 66.6 specimen is *M. volans*; if < 66.6 *M. lucifugus* or *M. yumanensis**

* To discriminate between *M. lucifugus* and *M. yumanensis*, see p. 61.

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